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·Review·

Functional neuroimaging of extraversion-introversion

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Neuroimaging techniques such as functional magnetic resonance imaging and positron emission tomography have provided an unprecedented neurobiological perspective for research on personality traits. Evidence from task-related neuroimaging has shown that extraversion is associated with activations in regions of the anterior cingulate cortex, dorsolateral prefrontal cortex, middle temporal gyrus and the amygdala. Currently, resting-state neuroimaging is being widely used in cognitive neuroscience. Initial exploration of extraversion has revealed correlations with the medial prefrontal cortex, anterior cingulate cortex, insular cortex, and the precuneus. Recent research work has indicated that the long-range temporal dependence of the resting-state spontaneous oscillation has high test-retest reliability. Moreover, the long-range temporal dependence of the resting-state networks is highly correlated with personality traits, and this can be used for the prediction of extraversion. As the long-range temporal dependence reflects real-time information updating in individuals, this method may provide a new approach to research on personality traits.

Keywords: extraversion; neuroimaging; resting-state fMRI; default mode network; scale-free dynamics

Introduction

In personality psychology, personality traits are regarded as an individual's lasting and stable behavioral tendencies at different times and in different situations. As one of the most important dimensions of personality traits, extraversion is the best established and validated[1]. Moreover, extraversion is the most stable core trait and a universal component in personality theory. Extraverts are typically described in positive emotional terms such as excitement, engagement, and enthusiasm. In contrast, introverts are described as quiet, conservative, and insensitive to the environment. An individual with high extraversion is more talkative, outgoing, and excited than someone with low extraversion, but even people with low extraversion may occasionally experience talkative and outgoing states. Trait levels of extraversion are known to be highly heritable and are linked to vulnerability to anxiety and major depression disorder[2,3]. Although much is known about the behavioral correlates of extraversion, little is understood about its biological basis.

Research on personality traits usually has the ambitious goal of providing a comprehensive understanding of a person’s integrated framework[3]. To achieve this goal, various effective research methods have been adopted. Based on the premise that the whole person cannot be understood without understanding the brain, personality neuroscience has emerged as an important direction in the study of personality traits[4]. Generally, personality traits are measured by questionnaire through self-report or peer-rating. Then, correlations between personality traits and neurobiological parameters are calculated[5]. Currently, a number of techniques are available for personality neuroscience. Anatomical neuroimaging, such as magnetic resonance imaging (MRI) and diffusion tensor imaging, allows the assessment of brain structure at high spatial resolution[6,7]. However, this review focuses on functional brain imaging modalities, such as electroencephalography (EEG), functional MRI (fMRI), and positron emission tomography (PET). Functional neuroimaging provides dynamic information on the activities of neurons or their populations during a perception or cognitive task. One of the most important challenges of functional neuroimaging in personality neuroscience is the localization of specific brain areas that underlie certain personality traits, and the monitoring of ongoing brain activity that causes individual differences in behavior.

Neuroimaging studies have indicated that multiple spatially-distributed regions are associated with extraversion (Fig. 1). Evidence from task-related neuroimaging revealed that extraversion is associated with activation in the posterior cingulate/precuneus (PCC), medial prefrontal cortex (mPFC), dorsolateral prefrontal cortex (dlPFC), anterior cingulate cortex (ACC), middle temporal gyrus (MTG), the amygdala, and the nucleus accumbens[8-10]. Furthermore, resting-state neuroimaging has revealed that spontaneous oscillations in the PCC, mPFC, orbitofrontal cortex, insula and hippocampus are significantly correlated with extraversion[11-13]. As both task-related and resting-state neuroimaging have revealed the importance of the PCC and mPFC, key regions of the default mode network (DMN), these results indicate a close relationship between the DMN and extraversion.

It is worth mentioning that resting-state neuroimaging is increasingly showing advantages[14]. Recent research work indicated that the temporal structure of resting-state spontaneous oscillation has high test-retest reliability[15-17]. The scale-free dynamics, indicated by the power spectrum with the formula $P \propto 1/f^{\beta}$, can be considered a measure of long-range temporal dependence (also called "long memory")[17]. As long memory reflects real-time information-updating in individuals, this method may provide a new approach to research on personality neuroscience[12].

The purpose of this review is to provide new insights into the neuronal activity underlying human personality traits. Here, we first summarize findings from both task-related and resting-state neuroimaging research on extraversion. Then a new analytical method for resting-state neuroscience, the long-range temporal dependence of the resting-state, is introduced.

Task-Related Neuroimaging of Extraversion

Previous neuroimaging experiments have demonstrated that some specific brain regions engaged in cognitive-affective tasks are associated with specific personality traits[4]. As extraversion is the primary manifestation in personality of sensitivity to rewarding and positive stimuli, paradigms involving decision-making and emotional regulation are widely used in this field[10, 18-20]. These studies showed that a wide range of brain regions are correlated with extraversion, such as the mPFC, ACC, and MTG[10, 18-20].

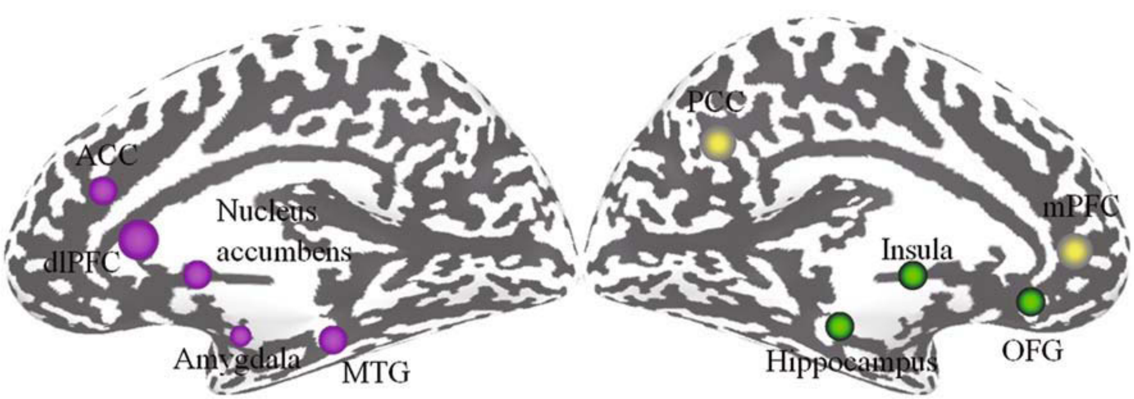

Fig. 1. Core brain regions associated with extraversion. Extraversion-related task and resting-state regions are represented by different colors. Task (pink): dlPFC, ACC, MTG, amygdala, and nucleus accumbens. Resting-state (green): OFC, insula, and hippocampus. Regions sensitive to both task and resting-state (yellow): mPFC and PCC. dlPFC, dorsolateral prefrontal cortex; ACC, anterior cingulate cortex; MTG, middle temporal gyrus; OFC, orbitofrontal cortex; mPFC, medial prefrontal cortex; PCC, posterior cingulate/precuneus.

Dopaminergic Function in Extraversion

Dopamine plays an important role in behaviors of reward and addiction that involve approaching potential rewards[21]. In fact, most sub-traits of extraversion, such as assertiveness and talkativeness, represent approach behavior. A growing body of evidence has shown that extraversion is influenced by the dopaminergic system[19, 22,23]. Previous task-related neuroimaging studies usually focused on the exploratory behavior of individuals with high extraversion[19, 22]. Current studies have shown that extraversion encompasses not only the traits reflecting wanting (such as assertiveness and driving to achieve a reward), but also the traits reflecting liking, such as positive emotionality and enjoyment of social interactions[10]. Both the wanting and liking traits are associated with the dopaminergic system around the nucleus accumbens and amygdala, crucial regions in motivation, emotion, and reward[19].

EEG and ERPs

EEG, or its derivative event-related potentials (ERPs), provide a measure of neuronal activity with the highest temporal resolution. EEG and ERPs are suitable for revealing the dynamic process of a psychophysical system in response to environmental stimulation[24]. Interestingly, personality is a reflection of this dynamic process, and hence it can be revealed by EEG measurements[25].

In Eysenck’s theory of extraversion, introverts demonstrate higher levels of basal activity, yielding higher tonic cortical arousal than extraverts[26]. Under this hypothesis, extraverts are conversely described to be chronically under-aroused and easily bored, and they show a low amplitude of basal activity in EEG and ERPs[27]. As the α rhythm (8–10 Hz) is a widely-accepted index of cortical arousal, eye-closed EEG has been widely used to explore the neuronal substrates of extraversion[28,29]. The α rhythm is also a stable dependent variable during working memory and one study has investigated the interactive effects of agentic extraversion and dopamine using spectral EEG[23]. This experiment contained four load-graded *n*-back working memory tasks[23]. The effects of the D2-dopamine antagonist sulpiride during the performance of working memory were analyzed by comparing participants with high *versus* low agentic extraversion. The results showed that the extraversion-related differences in the load-responsivity pattern were reversed by sulpiride, and the effect was especially large in frontal areas. A recent EEG study was extended to the θ rhythm (4–8 Hz) to investigate the interaction between personality and cognitive performance[30]. Intriguingly, this study showed that the source of intracerebral θ was localized within the rostral subdivisions of the ACC. The current density of θ within the rostral ACC was significantly correlated with the agentic extraversion spectrum, and had high retest stability during 5 h[30].

In addition, in a two-tone auditory discrimination task, undergraduate students were grouped into introverts and extraverts, and then performed a two-trial replication procedure[31]. The findings showed that P300 amplitudes did not interact with either the personality variable or the trial block variable[31]. Nevertheless, P300 amplitudes declined significantly from the early to the late blocks for extraverted participants, but did not show any change across trial blocks for introverted participants[31]. Further, female participants tended to have larger P300 amplitudes than their male counterparts, but the gender factor did not interact with either the personality variable or the trial block variable. This study suggested that ERP amplitude habituates more rapidly in extraverts than in introverts, and hence extraverts may get bored more quickly[31]. Given that extroverts' arousal patterns habituate so quickly, they may need more stimulation and have to seek more novel stimuli than introverts do in daily life[31]. However, although current EEG/ERP studies have shown that the α/θ rhythms and P300 are closely associated with extraversion, related studies have been relatively limited and do not provide a comprehensive understanding of personality. Therefore, further investigations should focus on ERPs in response to positive or rewarding stimuli, because of their advantages in the temporal domain.

fMRI

Functional MRI provides a high spatial resolution for brain function, which is important in localizing a certain personality trait within specific regions. By using task-related fMRI, studies have shown that extraversion is a basic dimension of personality that describes individual differences during perception or cognition tasks[10, 18-20]. The main brain structure engaged in cognition tasks is the frontoparietal network, which contains the dlPFC, insula, and ACC. In response to an inhibition task, self-reported levels of extraversion are closely associated with activations in the lateral regions of frontoparietal networks, which are typically associated with task-focused controlled processes. More precisely, extraversion is negatively correlated with the activity of the PFC when the oddball trials are compared to the non-oddball trials in the inhibition task[8]. In contrast, the dlPFC and ACC have positive correlations with extraversion during an *n*-back task[9]. During the *n*-back task, different loads are presented and extraversion is assessed as the scores on the Eysenck Personality Questionnaire. The results showed that participants with high extraversion have larger signal changes in the dlPFC and ACC from rest to the 3-back condition. Moreover, these studies suggest that individual differences may affect the brain's responses during cognitive activity, and provide evidence for the hypothesis that self-reported levels of extraversion may reflect individual differences in the cortical arousal system.

Besides executive-control tasks, extraversion is also associated with brain activities in the regions of ventral PFC, ACC, nucleus accumbens, and striatum in response to positive or rewarding stimuli[10, 18, 20]. For example, negative correlations have been found between extraversion and ventral PFC activity when rewarding stimuli are presented[10]. Negative correlations are also found in the rostral ACC and ventral striatum in response to positive faces[20] and favorite brands[19], respectively. Current research attempts to reveal the brain localization of narrowly-defined trait-facets that are part of extraversion. An event-related fMRI study used an emotional Stroop task to investigate the influence of extraversion on affective processing[18]. The results showed that individuals with higher extraversion scores have stronger functional connectivity between the ACC and the inferior parietal lobule. Moreover, this association could also be accounted for by the distinct facets of extraversion.

Taken together, these studies showed that the personality dimension of extraversion is negatively linked with the dopaminergic system, as well as multiple executive-control-related and reward-sensitive regions. In addition, the dimension of extraversion is a continuum; individuals with high extraversion scores prefer social interactions and are gregarious, while individuals with low extraversion scores prefer to avoid social interactions and are sensitive to emotional conflict[18]. Therefore, by comparing the neuronal activities of individuals high in extraversion and individuals low in extraversion, fMRI tasks may help reveal the neuronal mechanisms of extraversion.

Resting-State Neuroimaging of Extraversion

Resting-state neuroimaging has developed greatly over the 20 years since the identification of low-frequency spontaneous fluctuation in the sensorimotor cortex[32]. Different from the task- or stimulus-dependent state, the resting-state provides a new insight into the neuronal mechanisms that are involved in perpetuating the constant internal milieu and in specific personality traits[5]. In addition, given that spontaneous fluctuations consume >60% of the total energy of the brain[33], and the spontaneous activity at rest may be involved in the internal processes underlying the representation of self, separate from the environment[34], it is possible that the intrinsically-organized functional brain networks may have a direct relation with the personality[5, 12].

Recently, resting-state neuroimaging has gradually evolved into a powerful tool for investigating the neuronal correlates of extraversion. Previous studies have suggested that extraversion is associated with activities in the frontal and temporal areas[8, 25]. Recent studies have linked extraversion with functional connectivity, which examines the inter-regional temporal correlations between predefined seed regions and related functional regions[35,36]. One remarkable property of spontaneous brain activity is that it can be consistently segregated into multiple resting-state networks (RSNs)[37], which provides new insights into the large-scale neuronal representation of extraversion[12]. Here we introduce some methods of analysis in resting-state neuroscience and the related findings for extraversion.

PET

Earlier understanding of the resting-state brain activity of extraversion relied primarily on PET and single-photon emission computed tomography. PET measures the rate of blood flow through particular regions of the brain by means of short-lived isotopes that emit positrons. It provides functional information about the whole brain at a relatively high spatial resolution[38]. In one study, extraversion was shown to be associated with regional cerebral perfusion as well as regional cerebral glucose metabolism in the frontal and temporal regions[26]. Specifically, PET studies have provided some evidence regarding the association between extraversion and greater cerebral flow at rest, in regions such as the ACC, right insular cortex, bilateral temporal lobes, pulvinar nucleus of the thalamus, posterior parietal lobe, and the left amygdala[26, 38, 39]. Furthermore, extraversion also correlates with increased glucose metabolism in the orbitofrontal cortex[38] and the right putamen[40].

The DMN, probably the most widely studied functional network in resting-state neuroimaging, includes the PCC, mPFC, and angular gyrus[37]. These regions present high metabolic activity when the brain is at rest, or when individuals do not focus on any external demands. One PET study investigated the role of resting-state glucose metabolic activity in different brain regions in positive emotionality, a sub-dimension of extraversion, and found that positive emotionality was positively correlated with metabolism in regions within the DMN[41]. This finding indicates that increased activity of the DMN at rest may be a neurobiological marker for positive emotionality[41]. In line with resting-state fMRI studies which showed that the DMN is closely associated with personality traits, the DMN has also been implicated in a wide range of cognitive processes that embody personality traits, such as internal positive emotionality, autobiographical memory, and emotional processing[12, 35]. As researchers have put more emphasis on studies of large-scale networks in recent years, it is necessary to identify the brain correlates of a situation-independent personality at the large network scale[13]. Moreover, given that the DMN is among the stable large-scale brain networks in the resting state, it is possible to relate the DMN to a stable personality trait such as extraversion.

Regional Homogeneity

Instead of detecting the activated brain areas, resting-state fMRI reveals intrinsic spontaneous fluctuations while avoiding the constraints of task-based approaches[37]. In recent years, resting-state fMRI has opened up a new avenue for understanding the neurobiological substrates of extraversion. Compared with PET, the advantages of resting-state fMRI include minimally-invasive procedures and refined temporal and spatial resolution[37]. Recent resting-state fMRI studies have mainly focused on functional connectivity analyses, which examine the interregional temporal correlations between predefined seed regions and related functional regions. An alternative analysis measures the amplitude of low-frequency fluctuations (ALFF), which reflects the intensity of spontaneous neuronal activity at rest[42]. Another approach is to examine the regional homogeneity (ReHo), which evaluates the similarities of signals among neighbors[11]. In this section, we only introduce ReHo, while the following sections will focus on the ALFF and functional connectivity.

Based on an underlying assumption that brain activity is more likely to occur in clusters than in a single voxel, ReHo evaluates the similarities between the time series of a given voxel and its nearest neighbors[11]. One study has shown that ReHo is negatively correlated with extraversion in the mPFC, an important portion of the DMN, indicating a relationship between the DMN and extraversion[11]. In addition, the insula, cerebellum, and cingulate gyrus are positively correlated with extraversion, suggesting close associations between extraversion and the regions engaged in affective processing[11].

Amplitude of Low-Frequency Fluctuations

ALFF measures the amplitude of regional activity across a specific frequency range, and has been increasingly used in resting-state fMRI[42]. Two steps are included in the calculation of ALFF. First, the time series for each voxel is transformed to the frequency domain after signal pre-processing. Second, the square root of the power spectrum is averaged across 0.01–0.08 Hz at each voxel. Finally, the association between extraversion and ALFF is investigated using whole-brain correlation analysis.

In a recent study, participants completed the Five-Factor Inventory[43] and underwent a 5-min resting-state fMRI scan[42]. The results revealed significant correlations between extraversion and ALFF within the PCC, the striatum, and the superior frontal gyrus[42]. In addition, when analysis was focused on the relationships between extraversion and the DMN, extraversion was shown to be positively correlated with ALFF in the PCC and the mPFC, indicating major contributions of the midline core regions of the DMN to extraversion[13].

Since the frequency band used in ALFF (0.01–0.08 Hz) can be divided into distinct sub-frequency bands, the amplitude of regional activity was further investigated for Slow-5 (0.01–0.027 Hz) and Slow-4 (0.027–0.073 Hz)[44]. Slow-4 and Slow-5 have been identified as the primary oscillations in gray matter, and they have shown close relationships with specific properties such as extraversion[44, 45]. Slow-5 mainly exists within the default-mode regions, while Slow-4 is more robust around the basal ganglia[44]. In addition, Slow-4 is more reliable and has greater test-retest reliability than Slow-5. A previous study has demonstrated a positive correlation between Slow-5 and extraversion in the midline core regions of the DMN[45]. In contrast, Slow-4 is negatively associated with extraversion in the left hippocampus, implying that the neuronal circuitry of emotion influences personality traits[45].

Functional Connectivity

The aforementioned personality studies of resting-state neuroimaging have revealed close relationships between extraversion and focal brain activities, and they provide part of the perspective of functional segregation[46]. As a principle of organization in the human brain, functional segregation can link local foci of activity to extraversion scores. In contrast, functional connectivity focuses on the collaboration between regions[46]. As the human brain is a complex and efficient network, many cognitive functions, from internal coordination (interoception) to external monitoring (exteroception), are executed by the integration of functionally-specialized areas[47].

For example, using two cognitive and affective 'hubs' in the brain—the ACC and the PCC—as regions of interest, researchers have explored the functional connectivity between the ACC/PCC and other brain regions, as well as their relationships with extraversion[5]. They found that extraversion predicts the functional connectivity between seed regions and lateral paralimibic regions involved in reward and motivation[5]. Another study showed that intrinsic amygdala-cortical functional connectivity is closely associated with extraversion[48]. However, although the functional connectivity between different regions is an important neuronal correlate[5, 48], very little is known about the relationships between extraversion and large-scale networks (i.e., RSNs).

Recently, research has suggested that graph theoretical analysis provides a powerful framework to quantitatively characterize the properties of the functional connectivity on the scale of the whole brain[49]. Moreover, some researchers have linked personality traits with graph theory analyses, and found a positive association between extraversion and clustering coefficient values[36]. Because high clustering coefficients indicate that individual brain regions are more likely to be part of the same "neighborhood", brains with higher extraversion scores have more friendship circles than those with lower extraversion scores[36]. Although this study may give a new direction to personality research, studies on the extraversion-related properties of brain networks are relatively limited. This may be because these abstracted properties are unstable among participants and mutable in different situations[49]. In contrast, extraversion is a situation-independent personality trait. A promising direction for personality neuroscience is to reveal the contribution of different RSNs, which constitute the stable large-scale neuronal substrates of extraversion[13].

Scale-Free Oscillations and Extraversion

While spontaneous activity has been mainly investigated using measures of ReHo, ALFF, and functional connectivity, the dynamic properties of intrinsic brain activity are rarely investigated using these methods[5, 35, 47]. Recently, the Hurst exponent (H) has been accepted to quantize the scale-free properties of spontaneous activity[17]. Generally, H is defined by the power spectrum with the formula $P \propto 1/f^{\beta}$, and is considered to be a measure of long-range temporal dependence that is present in a random-walk process[17]. In addition, H has been used to locate a process on the continuum of randomness extending from Brownian motion (totally random) to Euclidian order (totally regular). An H closer to 0.5 indicates more randomness or chaos, whereas an H closer to 1 indicates more regular or persistent fluctuations[12, 50].

In healthy adults, studies have shown that the Hurst exponent of resting-state fMRI is usually between 0.7 and 0.8, with some properties of long memory[50]. Further, H decreases during task state[17]. The scale-free properties are also associated with disorders such as Alzheimer's disease[51] and autism[52]. Considering the non-pathological effects, normal aging is accompanied by an increase in long memory in the region of the hippocampus, whereas Gray's impulsivity score is associated with a decrease of H[53]. Recently, we validated that resting-state spontaneous oscillations in RSNs encode personality traits. Specifically, H predicts the individual variation of extraversion[12].

Below we describe our previous study on extraversion

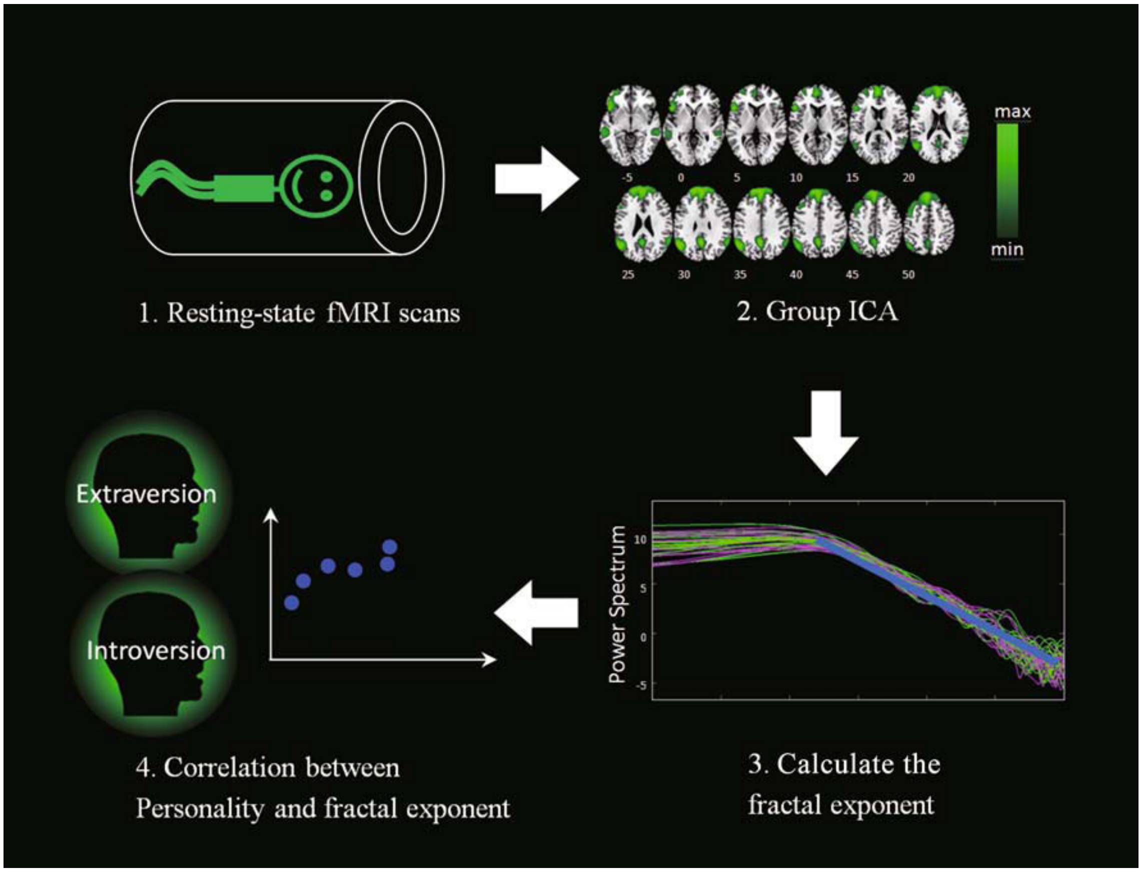

Fig. 2. Flowchart of scale-free analysis of resting state fMRI. First, functional neuroimaging data are acquired using resting-state fMRI. Second, all data are pre-processed and analyzed using group independent component analysis (ICA). Third, resting-state networks are extracted and the Hurst exponent is calculated for each network. Fourth, the Hurst exponents of resting-state networks are correlated with psychometric data.

using resting-state fMRI[12], not only to provide more details about resting-state neuroimaging studies of personality, but also to emphasize the importance of scale-free analysis. The basic processes are shown in Fig. 2.

Resting-State fMRI Acquisition

Healthy volunteers participated in this study. Each participant completed a self-report questionnaire, the Eysenck Personality Questionnaire-Revised, Short Scale for Chinese (EPQ-RSC)[1, 54]. The EPQ-RSC has two dimensions: extraversion and neuroticism. The overall mean score for extraversion was measured and then compared to the Chinese standardization group. Functional neuroimaging data were acquired using an fMRI scanner. Our recommended scanning length was 5 min, and the minimum functional volumes were 200 using an EPI sequence. During the resting-state scan, no specific instructions were given except to relax and stay still. Head movements were minimized using a cushioned head-fixation device.

Pre-processing and Group ICA

The main sources of noise during fMRI scan might be: (1) inter-individual differences in brain volume; (2) artifacts due to head motion; and (3) different acquisition times for each slice. Because MRI scans are usually affected by different types of noise, the BOLD signals need pre-processing to increase the signal-noise ratio. All data were pre-processed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm, Wellcome Department of Cognitive Neurology, London, UK). The pre-processing included slice timing, head-motion correction, spatial normalization, smoothing, and linear-trend removal.

Participants with large head motions were excluded.

Extracting resting-state networks from the fMRI data can be seen as a blind source separation problem. Here, we assumed that the spontaneous oscillations of the brain are independent of heartbeat, respiration, physiological activities of the body, and other external noise[55]. As a result, ICA, a data-driven approach, was used here to extract RSNs. The pre-processed data of all participants were further processed with group ICA (GIFT, http://icatb.sourceforge.net/)[55]. The optimal number of components was estimated using the minimum description length criterion. Independent components and their time-courses for each participant were back-reconstructed, and the mean spatial maps for each group were transformed to Z-scores for display.

Resting-State Networks

Nine independent components that corresponded to RSNs were identified (Fig. 3)[12]. Note that the nine selected networks corresponded to those components with the largest spatial correlations with the RSN templates[50]. These nine networks were as follows (see Fig. 3): a visual network that encompasses the medial part of the striate

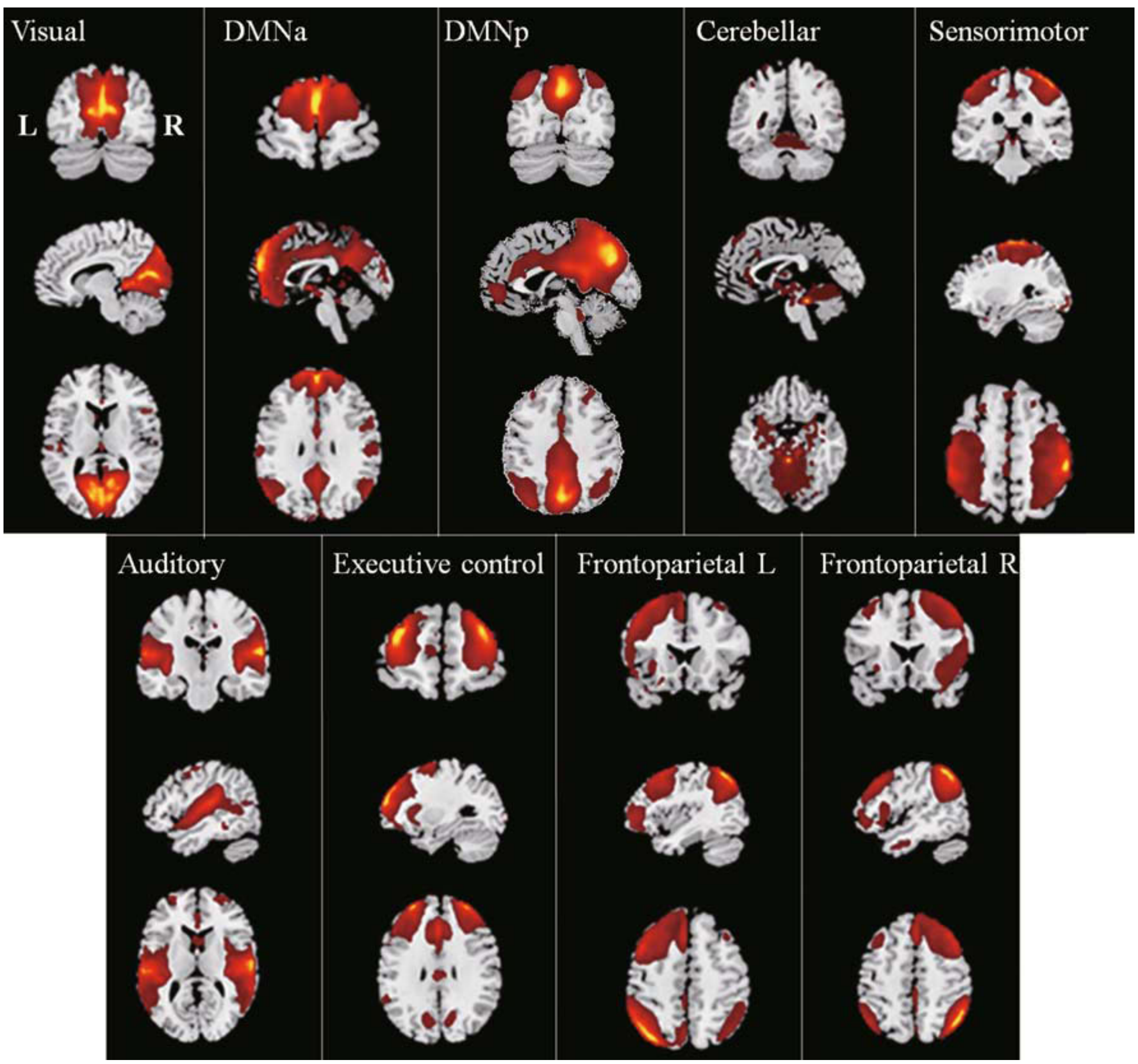

Fig. 3. Extraction of resting-state networks (RSNs). Nine RSNs were identified, as described in the text, including visual cortex, the anterior and posterior sub-networks of the default mode network (DMN), the cerebellar network, the sensorimotor and auditory cortical networks, the executive control network, and the left and right frontoparietal networks.

and parastriate regions (BA 17/18) in the occipital lobe, corresponding to the peripheral retinotopic representation; the anterior (DMNa) and posterior (DMNp) sub-networks of the DMN including the angular gyrus, the posterior cingulate (BA 23/39), frontopolar cortex (BA 10) and the superior parietal (BA 7) region; a cerebellar network and a sensorimotor network, which are spatially consistent with the bilateral sensorimotor cortices (BA 1/2/3); an auditory network spanning the auditory regions in the bilateral temporopolar and retrosubicular cortex (BA 38/48), as well as the sub-central area (BA 43); an executive control network spanning several medial–frontal areas, including the anterior cingulate and bilateral dorsolateral prefrontal cortex (BA 24/46); the left and right frontoparietal networks, which are lateralized and largely symmetrical with respect to the midline, including the bilateral angular gyrus, the right dorsolateral prefrontal cortex and the frontal eye field (BA 8/9/39). Note that these RSNs are consistent with the spatial patterns revealed during various cognitive tasks[14]. The corresponding time-course of each network is the input for Hurst estimation.

The Resting-State Fingerprint of Extraversion

To acquire the resting-state fingerprint of extraversion, first the Hurst exponent was calculated using the Wavelet Leader and Bootstrap-based MultiFractal analysis toolbox (http://perso.ens-lyon.fr/herwig.wendt/)[15]. Then, correlation analysis was performed between the scale parameters of the nine RSNs and psychometric data. The inclusion of Hurst exponents in all nine RSNs may help achieve a more accurate prediction of individual extraversion.

The correlation analysis showed that extraversion is significantly and negatively correlated with H in the DMN, the middle visual, and the right-lateralized frontoparietal networks (Fig. 4).

Because H is considered to be a measure of long-range temporal dependence[17], these results indicate that altered long memory in intrinsic neuronal activity is likely to be the neurophysiological mechanism that

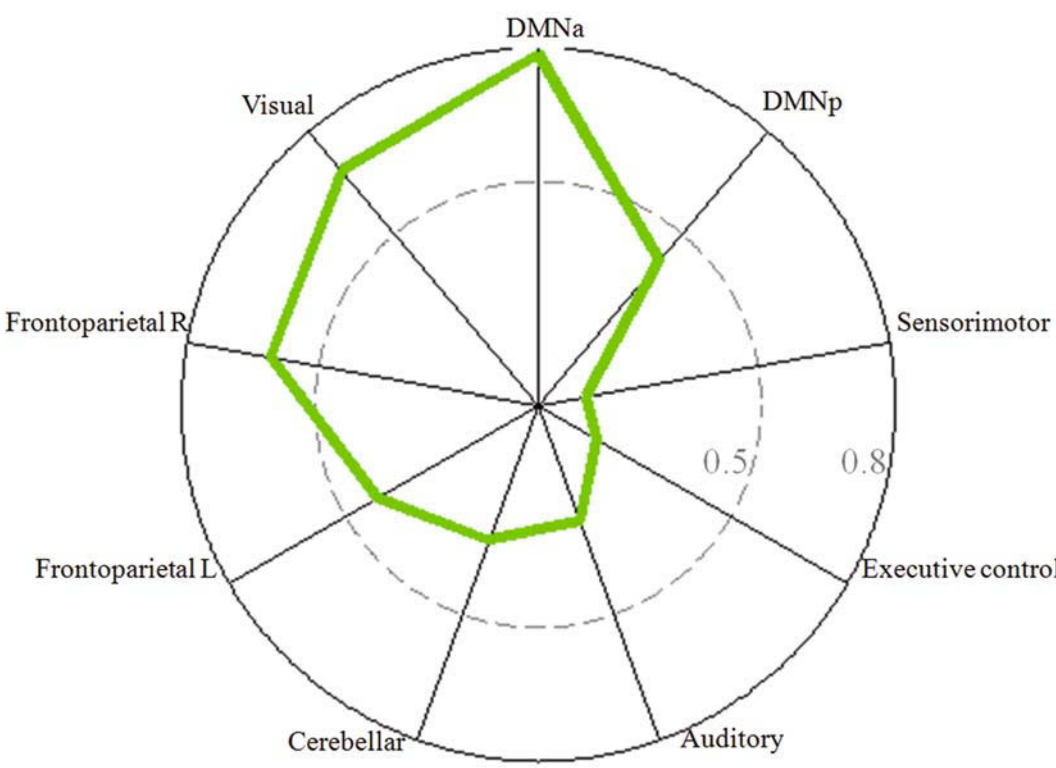

Fig. 4. The resting-state fingerprint of extraversion. Correlations between the Hurst exponents of 9 resting-state networks (see Fig. 3) and extraversion scores. Each spoke in the radar chart represented the absolute value of the Spearman rank-correlation. The spatial patterns of each network are shown in Fig. 3.

underpins the link between the fractal properties of RSNs and extraversion. Previous studies have speculated that the Hurst exponent represents the efficiency of online information processing[17]. A smaller value suggests that the system is more efficient in online information processing and has less temporal redundancy. Indeed, several previous studies have shown that the long memory of the fMRI signal decreases across widespread brain regions during the task state[15]. In contrast, the dynamic range of the fMRI signal is the largest and the temporal dependence is the longest during the resting state. Measurement of Hurst exponents using magnetoencephalography has also confirmed this phenomenon when contrasting resting-state activity with evoked activity during a learning paradigm[56]. In a remarkable parallel to these findings in healthy individuals, the Hurst exponent of the fMRI signal in Alzheimer patients is larger than that in age-matched controls, suggesting that the efficiency of information processing in these patients is reduced[51, 53]. Based on the above background, we speculate that individuals with higher extraversion scores would be more active in processing incoming information. In contrast, those with lower extraversion scores may be more concerned with long memory, and the past brain activity has a stronger influence on their future responses.

Perspectives

With the development of neuroimaging techniques such as fMRI and PET, studies of extraversion, as well as other personality variables, can be greatly improved. Evidence from both task and resting-state functional neuroimaging has identified a number of biological markers for extraversion. On one hand, these markers may lay the foundation for further prediction of individual behaviors; on the other hand, they may stimulate theoretical innovation in personality neuroscience.

Self-report measures have been the primary means of assessing personality constructs. Although they have served personality researchers well, they have also been criticized for being flawed and inaccurate. Rather than measuring the personality itself, self-reporting usually assesses the affective consequences of personality[12]. Furthermore, individuals who lack introspective access to their personality character may not be aware of the processes that lead to that state. In other words, the self-report scores may be a noisy output instead of a true reflection of personality. Because of the imprecision of self-reports, personality traits have limited success in predicting expected behavioral outcomes. In this context, investigating a potential link between personality and the fractal properties of resting-state dynamics using a correlative approach appears more promising for future personality neuroscience research, as subjective judgment is replaced by an objective physiological index.

Another disadvantage of self-report measures is that completing a personality questionnaire takes a long time. For example, the standard version of the Big Five has 120 questions, and usually half an hour is needed to complete the personality questionnaire. As an emerging technology, resting-state neuroimaging appears to be more effective. First, a resting-state scan of just 5-min can effectively acquire the fingerprints of personality traits. Second, the participants only need to stay still during the resting-state scanning. In addition, the implementation is simple and the main experiment does not need any professional knowledge or skills.

In a previous study, we investigated the potential link between personality and the fractal properties of RSNs using a correlative approach[12], highlighting the advantages of resting-state neuroimaging in the study of personality. Since RSNs are the full repertoire of functional networks used by the brain in action[14], we proposed to use a fingerprint of personality traits to fully illustrate the distribution of long memory in RSNs (see Fig. 4). The resting-state fingerprint may be a powerful tool to describe individual differences in personality traits, and how variations in brain organization and function affect personality traits such as extraversion. Our suggestions for future personality neuroscience research are to focus on the following three aspects.

First, the personality-related large-scale brain network needs to be identified. As for the associations between personality and the RSNs, personality traits are not simply associated with specific brain regions, but are encoded in a large-scale network that contains multiple brain regions. Thus, the perspective from the large-scale brain network is crucial to understanding personality. Current findings in resting-state neuroimaging support the idea that baseline activity in the DMN is related to individual differences in extraversion. Meanwhile, evidence from task-related neuroimaging revealed that extraversion is associated with the frontoparietal network[8,9]. Therefore, future studies should examine the relationships between these RSNs and personality traits when exploring the neuronal correlates of personality traits[57].

Second, data analysis methods, such as multivariate pattern analysis (MVPA), have provided a new plausible approach to characterize how information is represented and processed in the brain[58]. The ability to accurately predict the thoughts and actions of others is essential for successful social interactions[59]. In a recent fMRI study, participants were asked to learn the unique personality including agreeableness and extraversion of four protagonists, and then to imagine how each protagonist would behave in different scenarios[59]. Using MVPA, researchers found that the activity patterns in the medial prefrontal cortex accurately infer the personality of each protagonist, which provides novel evidence that brain activity can reveal whom someone is thinking about[59]. Because MVPA has advantages in revealing how information is represented and processed and its feasibility in the study of personality neuroscience has been indicated, we should make the best use of this technique to obtain the biological markers of personality traits.

Third, the contributions of different neuroimaging techniques should be clarified in personality research. The spatial resolution of EEG is relatively poor because of the influence of skull volume conduction on electrical potentials. Although many EEG and ERP studies have revealed the link between extraversion and cortical arousal, the corresponding brain regions are hard to localize with these techniques[25, 27-29]. In contrast, fMRI has higher spatial resolution than EEG or ERPs. But fMRI is an indirect measurement of neuronal activity, and is affected by many factors such as blood volume, flow rate, and the oxygen content of the blood[60]. In addition, although an entire brain volume can be captured in less than 65 ms using current fMRI scanners, the problem of limited temporal resolution is unsolved. Due to their respective strengths in the spatial and temporal domains, the integration of EEG and fMRI have provided a combined imaging with detailed electrophysiology and metabolic information[35, 50]. Spatial-temporal EEG/fMRI fusion (STEFF) uses the fusion of spatial constraint and temporal prediction in parallel, and can achieve a higher spatiotemporal resolution than each modality separately[60]. Based on STEFF, more model-specific evidence, such as the α rhythm in EEG and the RSNs in fMRI, may converge to a uniform neurobiological source of personality traits.

Finally, the research discussed above can be seen as an urge to use more sophisticated task paradigms in personality neuroscience with combined resting-state recordings. In a previous study, Sheng *et al.* used speech production tasks to investigate the relationship between personality traits and deactivation of the DMN[61]. They found that deactivations of posteromedial cortex predicted traits related to egocentricity, while deactivations of the mPFC predicted traits related to decision-making. These results are consistent with previous studies indicating that the DMN and the prefrontal cortex are associated with processes involving self-relevancy and affective decision-making. Because the DMN is a network that presents high activity during the resting-state[12, 41], these findings point out an important direction for future neuroimaging: combining tasks with resting-state neuroimaging.

With the rapid development of neuroimaging, more sophisticated functional imaging technologies may be used in personality neuroscience. Such studies linking the full repertoire of RSNs with personality traits are needed to investigate the fingerprints of personality traits. Moreover, neuroimaging techniques applied to personality traits have improved our understanding of the personality. For the foreseeable future, new theories of personality may emerge based on the growing body of neuronal evidence.

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