

Salience network dynamics underlying successful resistance of temptation

Rosa Steimke,^{1,2,3,4,5} Jason S. Nomi,⁵ Vince D. Calhoun,^{6,7} Christine Stelzel,^{1,8} Lena M. Paschke,¹ Robert Gaschler,⁹ Thomas Goschke,² Henrik Walter,^{1,3} and Lucina Q. Uddin^{5,10}

¹Division of Mind and Brain Research, Department of Psychiatry and Psychotherapy CCM, Charité - Universitätsmedizin Berlin, corporate member of Freie Universität Berlin, Humboldt - Universität zu Berlin, and Berlin Institute of Health, Berlin, Germany, ²Department of Psychology, Technische Universität Dresden, Dresden, Germany, ³Berlin School of Mind and Brain and ⁴Department of Psychology, Humboldt-Universität zu Berlin, Berlin, Germany, ⁵Department of Psychology, University of Miami, Coral Gables, FL, USA, ⁶The Mind Research Network, Albuquerque, NM 87106, ⁷Department of Electrical and Computer Engineering, The University of New Mexico, Albuquerque, NM 87131, USA, ⁸International Psychoanalytic University Berlin, Berlin, Germany, ⁹Department of Psychology, FernUniversität, Hagen, Hagen, Germany, and ¹⁰Neuroscience Program, University of Miami Miller School of Medicine, Miami, FL, USA

Henrik Walter and Lucina Q. Uddin authors contributed equally to this study.

Correspondence should be addressed to Lucina Uddin, Department of Psychology, University of Miami, P.O. Box 248185, Coral Gables, FL 33124, USA.
E-mail: luddin@miami.edu

Abstract

Self-control and the ability to resist temptation are critical for successful completion of long-term goals. Contemporary models in cognitive neuroscience emphasize the primary role of prefrontal cognitive control networks in aligning behavior with such goals. Here, we use gaze pattern analysis and dynamic functional connectivity fMRI data to explore how individual differences in the ability to resist temptation are related to intrinsic brain dynamics of the cognitive control and salience networks. Behaviorally, individuals exhibit greater gaze distance from target location (e.g. higher distractibility) during presentation of tempting erotic images compared with neutral images. Individuals whose intrinsic dynamic functional connectivity patterns gravitate toward configurations in which salience detection systems are less strongly coupled with visual systems resist tempting distractors more effectively. The ability to resist tempting distractors was not significantly related to intrinsic dynamics of the cognitive control network. These results suggest that susceptibility to temptation is governed in part by individual differences in salience network dynamics and provide novel evidence for involvement of brain systems outside canonical cognitive control networks in contributing to individual differences in self-control.

Key words: salience network; dynamic functional connectivity; self-control; temptation; resting-state fMRI

Received: 5 March 2017; Revised: 28 September 2017; Accepted: 16 October 2017

© The Author (2017). Published by Oxford University Press.

This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact journals.permissions@oup.com

Introduction

In our daily lives, we constantly encounter situations that evoke conflicting response tendencies: on the one hand impulsive reactions toward tempting stimuli and on the other hand actions that serve the realization of previously set goals (Hofmann et al., 2012). Self-control is correlated with well-being (Hofmann et al., 2014), and self-control failure has been related to addiction, obesity, post-traumatic stress disorder, depression and attention-deficit hyperactivity disorder (Schweitzer and Sulzer-Azaroff, 1995; Bechara, 2005; Kontinen et al., 2009; Walter et al., 2010; Özdemir et al., 2014). It is of great scientific interest to understand why some individuals are able to resist when faced with temptation, while others fail.

Erotic and sensual images are powerful visual temptations. The advertisement industry frequently makes use of erotic images (Reichert and Carpenter, 2004) because they are very salient and trigger us to involuntarily look toward them (Sennwald et al., 2016). This might be the case because they trigger evolutionarily meaningful attention allocation and approach behaviors (Fromberger et al., 2012). Here, we investigate the neural basis for individual differences in self-control in the face of temptation using a combination of eyetracking and dynamic functional connectivity fMRI.

The most prominent model of self-control is the dual-systems approach, which assumes that a reflective system serving higher-level goal representations can exert control over an impulsive system that reacts to stimuli in a direct automatic manner (e.g. Metcalfe and Mischel, 1999; Strack and Deutsch, 2004; Hofmann et al., 2009). The reflective system has been mainly associated with frontoparietal cognitive control networks (CCNs), while the impulsive system has been linked with visceral and sensory regions (McClure and Bickel, 2014). Prefrontal cortical regions have been associated with self-control (Hare et al., 2009; Hayashi et al., 2013). Based on this model, the CCN is a prime candidate for studying individual differences in self-control.

Another potential candidate for explaining individual differences in self-control is the salience network (SN). The SN is comprised of bilateral insula, dorsal anterior cingulate cortex (dACC) and other subcortical and limbic structures (Seeley et al., 2007) and is implicated in the direction of attention toward important stimuli and integration of top-down appraisal and bottom-up visceral and sensory information [see Uddin (2015), for review]. This central role in integrating information is reflected in its unique functional and structural connectivity profile. For example, the different insular nodes within the SN are associated with distinct functional connectivity profiles; the dorsal anterior insular cortex coactivates with areas associated with cognitive processing, the ventral anterior insular coactivates with areas associated with affective processing and the posterior insular coactivates with sensorimotor processing areas (Chang et al., 2013; Uddin et al., 2014).

In the task presented here, attention allocation toward task relevant information is in conflict with attention allocation toward task irrelevant, yet intrinsically relevant, information (e.g. erotic distractors). As the SN has been implicated in the allocation of attention toward task relevant information by interacting with other networks, and the coordination of neural resources (Uddin, 2015), individual differences in SN functioning might play an important role in explaining why some participants stay on task while others yield to the erotic distraction.

Most self-control research has focused on the downregulation of impulses by CCNs when examining individual

differences in self-control, while studies of bottom-up processes that influence self-control are underrepresented (but see Ludwig et al., 2013; Steimke et al., 2016). Task-based fMRI studies have indicated that self-control involves dorsolateral prefrontal cortex modulation of a value signal in the ventromedial prefrontal cortex (Hare et al., 2009). Recently, spontaneous fluctuations in resting-state brain activity have been shown to demonstrate reproducible correlations across brain regions organized into networks (Shehzad et al., 2009). Because resting-state networks are thought to represent individual differences in the brain's functional organization, resting-state fMRI has become a leading approach for understanding individual differences in behavior (Dubois and Adolphs, 2016).

Dynamic functional connectivity of resting-state fMRI data is a new approach that accounts for the non-stationarity of brain signals and enables the study of brain dynamics underlying behavior. Whereas the static functional connectivity approach assumes that the connectivity pattern of the brain remains stable over time, the dynamic functional connectivity approach accounts for moment-to-moment variability in connectivity profiles. Within this framework, the brain engages in reoccurring time-varying functional relations that can be referred to as functional connectivity 'states' (Hutchison et al., 2013; Calhoun et al., 2014). By taking time variation into account, the dynamic approach can give a more nuanced understanding of brain connectivity, which is vital for understanding the source of individual differences. Our previous work examining the dynamic functional connectivity profile of different insular subregions found partially distinct and partially overlapping dynamic state profiles of the anterior, ventral and posterior insular subdivisions, highlighting aspects of SN dynamics that have been previously overlooked (Nomi et al., 2016). Whole-brain dynamic state characteristics are related to individual differences in executive function (Jia et al., 2014; Yang et al., 2014; Nomi et al., 2017) as well as mental illnesses including schizophrenia and bipolar affective disorder (Damaraju et al., 2014; Rashid et al., 2014). No previous studies have considered the relationship between SN dynamics and self-control.

Here, we present results of a study examining the relationship between brain network dynamics and self-control in the face of temptation. Broadly, we expected that susceptibility to interference from visual distraction would be reflected in brain network dynamics. We predicted that individual differences in self-control would be related to CCN dynamics, SN dynamics or both. We explored these potential mechanisms underlying individual differences in self-control in a relatively large sample of 94 adults.

Materials and methods

Participants

Ninety-four current or former university or college students (Mean age = 25.93, s.d. = 3.84; 54 females) were included in the analysis. These data were part of a larger dataset of 126 participants who also completed additional fMRI tasks, self-control and cognitive control paradigms (Paschke et al., 2016; Sekutowicz et al., 2016). Of all participants, 109 had valid behavioral and eyetracking data (Steimke et al., 2016). Fifteen participants were excluded because either the fMRI registration process was not successful or because the fMRI scans did not cover the whole brain.

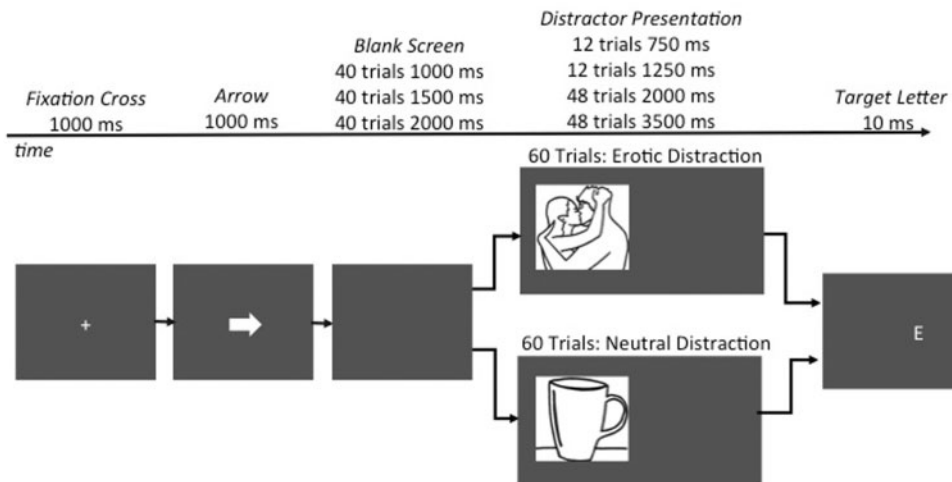


Fig. 1. Timing of behavioral experiment. A trial starts with a fixation cross. The fixation cross is followed by an arrow indicating the location of the next target letter 'E' or 'F' presented 5.9° of visual angle left or right from the center. After the arrow presentation, a cleared screen is presented for variable delay. Afterwards either a neutral or an erotic distractor is presented for a variable duration immediately followed by the target letter. Drawings are placeholders for photographs from the international affective picture system (Lang et al., 2008) and the internet.

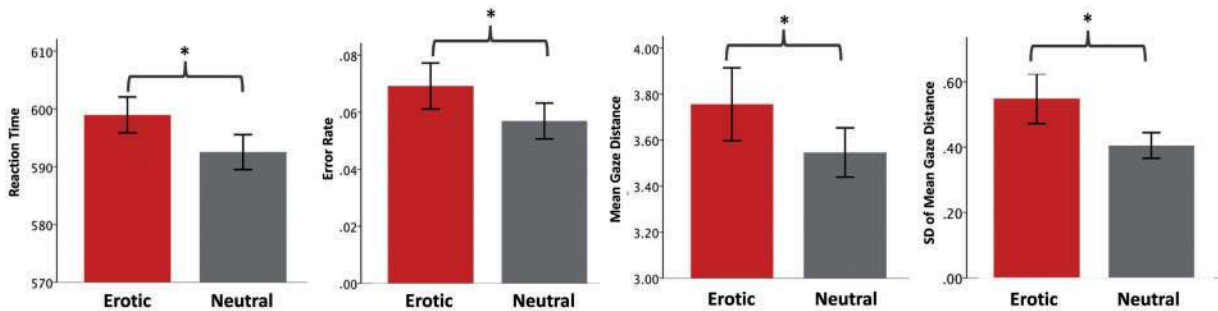


Fig. 2. Behavioral and eyetracking data. Mean reaction times, percent errors, gaze distance and standard deviation of the gaze distance (s.d.). Asterisks (*) indicate a significant difference at $P < 0.05$. Error bars represent the 95% confidence interval for within-subjects comparisons (Loftus and Masson, 1994).

Self-control task

In a task designed to assess self-control, participants were instructed to attend to a cued target location (left or right side of the screen) while facing the challenge to sustain attention despite neutral and erotic pictures presented as distractors on the other side of the screen [Figures 1 and 2; see Steimke et al. (2016) for behavioral and eyetracking results of the task]. Eyetracking data were acquired using a video-based eyetracker (sampling rate: 250 Hz spatial resolution: 0.05°, Cambridge Research Systems, UK). Participants were seated 36 cm from the screen. To reduce movement, participants were instructed to rest their chin and forehead on a chin rest. The distracting images were presented for a variable duration and elicited participants' eye gaze to shift away from the cued target location, resulting in poorer performance on the task, which was to identify by button press whether a white target letter was an 'E' or an 'F'. Variable distractor durations were introduced to prevent participants from anticipating when the target letter would be presented. Motivation of participants to perform accurately on the task was enhanced by offering the chance of a 10 Euro reward for accurate performance on one trial, which was randomly selected after completion of the task. Target letters were presented for 10 ms against a dark gray background, and participants were instructed to respond as quickly and accurately as possible. The distractors consisted of neutral pictures (e.g.

neutrally rated objects or scenes) and erotic pictures (pictures of couples in erotic situations) displayed on the contralateral side of the screen relative to the target location. Note that the task also included other conditions. Specifically, it included a condition with disgusting pictures presented before target letter presentation in the same location as the target letter, an additional condition with the same timing and location but involving neutral pictures, and a condition where no distractors were presented. To ensure the absence of carryover effects, the order of presentation was counterbalanced across conditions. Pictures were selected on the basis of valence, arousal and attraction ratings from 96 independent participants and erotic and neutral pictures were matched for brightness and complexity. Brightness and complexity (entropy in bits) was estimated using the Matlab image processing toolbox. Eye gaze distance from target location was used as a dependent variable. Specifically, the gaze distance difference score between trials with erotic and trials with neutral distraction was used. Gaze distance was used, as it is the most direct measure distractibility. Additionally, it was found that gaze distance, not reaction time, was related to delay of gratification in this task: participants who couldn't resist to eat one sweet immediately instead of waiting for two sweets after 45 min also showed greater gaze distance from target when erotic pictures were presented than participants who chose to wait (Steimke et al., 2016). A short test

of fluid intelligence [Leistungsprüfsystem (LPS) Unterteil 3, Horn (1983)] was performed to be able to control for individual differences in intelligence.

fMRI data acquisition and preprocessing

Each participant underwent resting-state fMRI scans during which they kept their eyes open and fixated on a fixation cross. Whole-brain fMRI data were collected with a 3 Tesla Siemens Tim Trio magnetic resonance imaging (MRI) scanner (Siemens, Erlangen, Germany) on a separate day from the behavioral testing. Using a 12-channel head coil, 32 slices were acquired in descending order with a T2*-sensitive one-shot gradient-echo echo-planar sequence. To minimize motion, the head was fixated with cushions. The following parameters were used: repetition time of 2 s, echo time of 25 ms, flip angle of 78°, data acquisition matrix of 64×64 , field of view of 24 cm, voxel size of $3 \times 3 \times 3$ mm and an interslice gap of 0.75 mm, 180 volumes. Preprocessing was performed with the Data Processing Assistant for Resting-state fMRI (<http://restfmri.net>). To ensure data were at signal equilibrium, the first 10 volumes were removed. Slice time correction was performed, and the data were realigned, normalized to an echo planar imaging (EPI) template and smoothed with a 8 mm Gaussian kernel.

Independent component analysis and static resting-state connectivity analysis

The first step in the dynamic functional network connectivity (dFNC) analysis was to parcellate the brain into regions of interest using a high-model order group independent component analysis (ICA) implemented with the group ICA of fMRI toolbox (GIFT) toolbox (<http://mialab.mrm.org/software/gift/>) using the infomax algorithm (Calhoun et al., 2001; Calhoun and Adali, 2012). A high-model order of 100 independent components (ICs) was chosen based on previous work demonstrating that this number of components sufficiently parcellates major brain networks [default mode network (DMN); CCN and SN] into individual brain areas that allows for more fine grained examination of network node interactions (Kiviniemi et al., 2009; Damaraju et al., 2014). Additional research demonstrates that model orders of 100 and below have better reproducibility than model orders higher than 100 (Abou-Elseoud et al., 2010). Stability of ICs was ensured by repeating the infomax algorithm 10 times using ICASSO and selecting the central run for further analysis. Subject specific spatial maps and time courses were back-reconstructed using the GICA1 method (Erhardt et al., 2011).

The ICA produced 100 ICs that were then subjected to visual inspection to eliminate components containing white matter, cerebral spinal fluid, movement or large amounts of high-frequency information (Damoiseaux et al., 2006; Allen et al., 2011). The SN and CCN nodes were selected on the basis of previous literature showing that bilateral insular regions and dorsal ACC are key regions for salience processing (Seeley et al., 2007), and bilateral dorsolateral prefrontal cortex and lateral parietal regions are key regions for a variety of cognitive tasks (Niendam et al., 2012). Note that in the meta-analysis by Niendam et al. (2012), the dorsal ACC is also implicated in cognitive control. However, this mostly applies to inhibition tasks, where a conflict between task demands and a competing salient response is being resolved. Because of the involvement of salience processing in these kinds of tasks, we assigned this region to the SN. For enabling easier interpretation of network structure within the correlation matrices, all remaining nodes were

sorted by visual inspection: visual network, components of the temporal lobes, DMN, components of the cerebellum and a sub-cortical network (Figure 3A). Traditional static functional connectivity analysis was performed using the GIFT toolbox (MANCOVA) adding gaze distance as a covariate of interest. The correlation matrix representing overall strength of coupling between these ICs can be seen in Figure 3B.

Independent component post-processing

Post-processing of non-noise ICs in GIFT consisted of despiking, detrending (linear, cubic and quadratic), regression of the Friston 24 motion parameters and a low pass filter (0.15 Hz). Despiking replaces outliers in IC time courses larger than the absolute median deviation with a third-order spline fit to clean portions of the data using AFNI's 3dDespike algorithm. Despiking decreases the temporal derivative (DVARs) (Power et al., 2011) over IC time courses and eliminates artifacts in dFNC analyses (Damaraju et al., 2014).

Sliding window analysis

Post-processed IC time courses were analyzed by using a sliding window dFNC algorithm in GIFT using window sizes of 22 TRs (44 s) slid in 1 repetition time (TR). A window size of 44 s was chosen as previous dFNC work utilized window sizes of 44 (Yang et al., 2014) and 45 s (Damaraju et al., 2014). Furthermore, previous dFNC research has demonstrated that window sizes of 30–60 s capture distinct dynamic functional connections not found in larger window sizes (Hutchison et al., 2013; Damaraju et al., 2014), methodological dFNC work has shown that such window sizes represent real fluctuations in functional connectivity (Sakoglu et al., 2010; Leonardi and Van De Ville, 2015). Additional empirical research demonstrates that these window sizes are able to capture cognitive states (Shirer et al., 2012; Wilson et al., 2015).

A tapered window consisting of a rectangle convolved with a Gaussian ($\sigma = 3$) was utilized to account for the limited number of time points in each sliding window. This produced a covariance matrix with the dimensions of 946 (sliding windows) \times 148 (paired connections) per subject. To further account for noise that may arise from a limited number of time points, each covariance matrix was regularized using the graphical LASSO method (L1 norm) (Friedman et al., 2008) of the inverse covariance matrix resulting in a correlation matrix (Damaraju et al., 2014).

CCN and SN dynamic states

Windowed correlation matrices for components within the CCN and SN were extracted and subjected to k-means clustering independently. The SN consisted of the bilateral insular, the dACC and the orbitofrontal cortex; the CCN consisted of bilateral dorsolateral prefrontal and parietal regions (see Figure 3A for SN and CCN nodes and Figure 3B for the extracted matrices). To be able to perform k-means clustering, the sliding windows of all participants were concatenated for the CCN and SN separately. Using these concatenated SN and concatenated CCNs, the number of optimal number of clusters was determined by using the elbow criterion applied to the cluster validity index derived from k-means clustering using 'city block' distance function (Allen et al., 2014) performed for clustering values between 2 and 20. This analysis revealed that five is the optimal number of clusters for the SN as well as for the

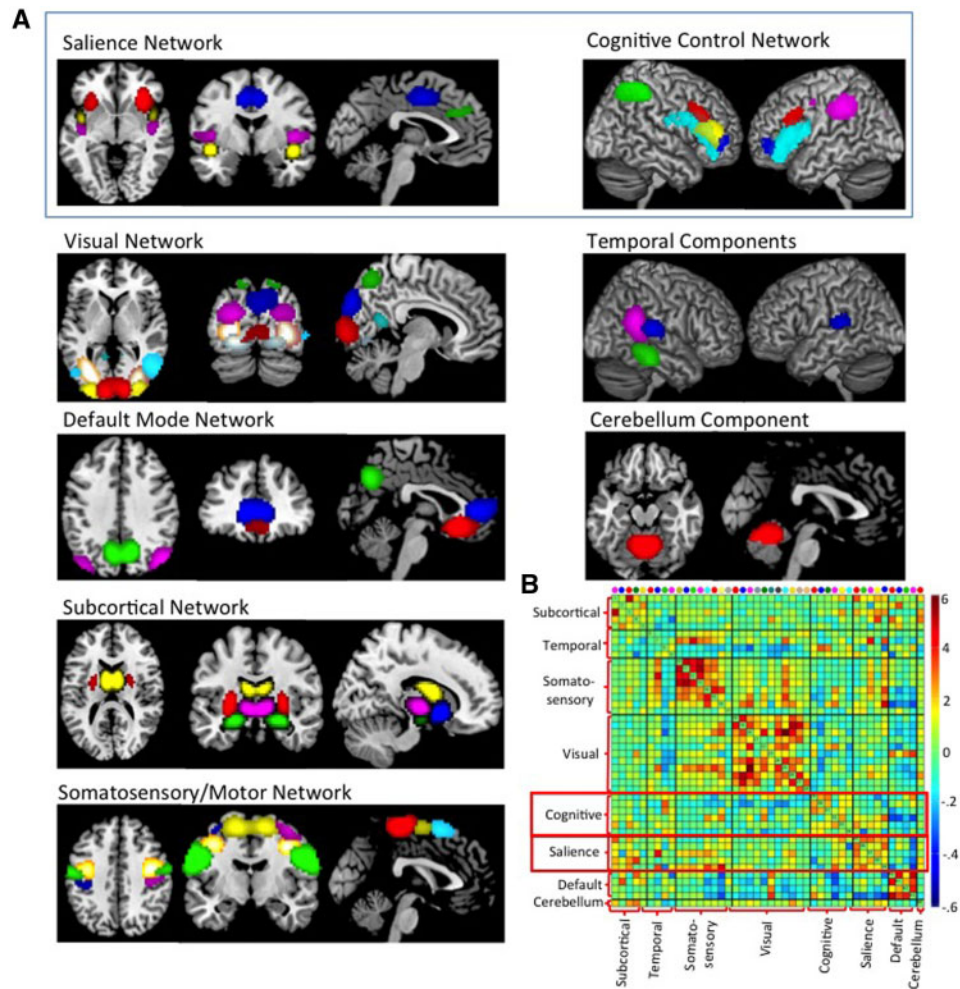


Fig. 3. Brain networks and static connectivity. (A) Display of the nodes identified by the ICA grouped into functional networks; each color represents a node within the network. (B) Static whole-brain functional connectivity correlation matrix; CCN and SNs used in the dynamic resting-state analysis are highlighted by red boxes. The color coding on top of the correlation matrix in Figure 3B corresponds to the colors of the brain areas of the different ICs in Figure 3A.

Table 1. Mean (*M*), s.d., paired sample *t*-test results (*t*-value and *P*-value) and effect size (η^2) for proportion of errors (Errors), reaction time in milliseconds (RT), mean gaze distance from target location (Mean Gaze) and the s.d. of the gaze distance from target location (s.d. Gaze) in degrees of the visual angle for the behavioral task

	Erotic <i>M</i> (s.d.)	Neutral <i>M</i> (s.d.)	<i>t</i> -value	<i>P</i> -value	η^2
Error	0.06(0.067)	0.05(0.05)	2.27	0.026	0.05
RT	594.62(64.39)	587.16(63.21)	3.30	0.001	0.10
Mean gaze	3.64(2.06)	3.43(1.8)	3.36	0.001	0.11
s.d. gaze	0.51(0.62)	0.39(0.42)	3.30	0.003	0.09

CCN, therefore the five cluster solutions for all results are presented.

For each of the 5 cognitive network and the 5 SN states, frequency and dwell time were calculated. Frequency was calculated as the percent that a brain state prevailed throughout the duration of the scan. Dwell time was calculated as the average length, measured in number of sliding windows, that a participant stayed in a given brain state. Pearson correlations were calculated to relate frequency and dwell time of cognitive network and SN states to distractibility by erotic temptation.

Results

Behavioral task results and static connectivity

In Figure 2, the reaction times, error rates, gaze distance and standard deviation of the gaze distance are presented. All of these measures revealed a significant difference between the erotic and the neutral condition at a threshold of $P < 0.05$ (Table 1). Note, that the error rates are low, potentially pointing toward a ceiling effect. As expected, the error rate for the temptation effect (error rates for the temptation condition minus error rates for the neutral condition) is positively and

significantly correlated with the gaze distance for the temptation effect (gaze distance from target location in the temptation condition minus gaze distance from target location in the neutral condition), $r = 0.275$, $P = 0.007$.

Correlations between frequency and dwell time demonstrate a significant positive relationship between the two measures (Supplementary Table S1). For a factor analysis, combining frequency and dwell time to a single compound score for each state see Supplementary Tables S1–S4. Performing the traditional static functional connectivity analysis with gaze distance as a covariate revealed no significant correlations at a P -value < 0.05 with false discovery rate (FDR) correction for multiple comparisons.

Dynamic SN states

We identified five different SN states (Figure 4A). Note that the states are sorted by the average percent of time participants spent in each of the five states. On average, participants spent 39.53 percent of their time in state 1 (s.d. = 27.54), 16.55 percent of their time in state 2 (s.d. = 16.59), 16.02 percent of their time in state 3 (s.d. = 15.72), 15.53 of their time in state 4 (s.d. = 17.06) and 12.37 percent of the time in state 5 (s.d. = 16.15). Repeating of k-means clustering to a total of five estimates revealed stability of the results (Table 2). Considering the frequency spent in each state, there is a floor effect for some participants, meaning they did not spend any time in that state at all. Five participants did not enter into state 1, 21 participants did not enter into state 2, 22 participants did not enter into state 3, 19 did not enter into state 4 and 33 did not enter into state 5. Not all participants enter into each state because k-means clustering of the concatenated data matrix including all subjects allows for the possibility that individual subjects will not contribute to each state (Damaraju et al., 2015; Nomi et al., 2016, 2017). The dwell time on average was 22.56 (s.d. = 26.00) for state 1, 10.87 (s.d. = 8.97) for state 2, 9.50 (s.d. = 8.25) for state 3, 9.70 (s.d. = 9.53) for state 4 and 9.98 (s.d. = 12.45) for state 5.

Dynamic CCN states

We identified five different CCN states (Figure 4B). The states are sorted by the average percent of time participants spent in each of the five states. On average, the participants spent 34.74 percent in state 1 (s.d. = 26.21), 17.98 percent of their time in state 2 (s.d. = 17.52), 17.92 percent in state 3 (s.d. = 17.67), 17.14 percent in state 4 (s.d. = 17.97) and 12.22 percent of their time in state 5 (s.d. = 13.84). Repeating of k-means clustering to a total of five estimates revealed stability of the results (Table 3). Concerning the frequency, 3 participants did not adopt state 1, 20 participants did not adopt state 2, 18 participants did not adopt state 3, 18 did not adopt state 4 and 28 did not adopt state 5. The dwell time on average was 20.65 (s.d. = 26.37) for state 1, 10.96 (s.d. = 10.52) for state 2, 10.93 (s.d. = 8.35) for state 3, 11.90 (s.d. = 11.37) for state 4 and 10.76 (s.d. = 11.19) for state 5.

Correlations with eye gaze behavior

As reported in a published paper describing behavioral results (Steimke et al., 2016), distracting images elicited participants' eye gaze to shift away from the target location, resulting in poorer performance on the task (Figure 2). Difficulty resisting temptations as indicated by gaze distance difference between erotic and neutral distractors was negatively correlated with the time spent in SN state 4, $r(92) = -0.26$, $P = 0.012$. This correlation remains significant when using the robust Spearman's Rank

correlation coefficient [$r_s(92) = -0.251$, $P = 0.015$]. To identify influential outliers, the Mahalanobis distance was calculated. The analysis revealed two outliers ($\chi^2 = 13$, 95; $\chi^2 = 16$, 18) at a threshold of $P < 0.001$. Excluding these two outliers reveals that the correlation between salience state 4 and temptation gaze effect remains significant ($r = -0.22$, $P = 0.034$).

The Pearson's correlation remained significant when excluding participants who did not spend any time in state 4, $r(73) = -0.25$, $P = 0.031$. Comparing participants who did not adopt state 4 at all with those who did enter state 4, using between group t-tests, revealed marginally significant higher distraction by temptation for participants who adopted state 4, $t(91) = 1.98$, $P = 0.051$. State 4 represents a dynamic functional connectivity state wherein the SN was negatively correlated with the visual network. All other states were not significantly correlated with performance on the temptation task (Figure 5A). Post hoc analysis revealed that time spent in state 4 was negatively correlated with time spent in state 1 [$r(92) = -0.36$, $P < 0.001$]. Further post hoc testing revealed that the significant negative correlation between time spent in state 4 and ability to resist temptation remained significant when controlling for age, gender and fluid intelligence as measured by LPS ($r = -0.276$, $P = 0.008$, $df = 89$). Correlating dwell time of the five SN states with the ability to resist temptations revealed the same pattern as for frequency: state 4 showed a significant negative correlation, while the others did not (Figure 5B). The correlation was also significant when using the robust Spearman's Rank correlation coefficient [$r_s(92) = -0.24$, $P = 0.02$].

There was no correlation between frequency or dwell time of any of the five CCN states with self-control in the face of temptation (Figure 6A and B).

Correlations with error rates

Difficulty resisting temptation as indicated by the error rate difference between erotic and neutral distractors was negatively correlated with the time spent in cognitive network state 1 ($r = 0.20$, $P = 0.048$). However, as displayed in Supplementary Figure S1, this might have been caused by a few influential cases. To test the robustness of this finding, we therefore used a non-parametric Spearman rank order correlation. The results reveal that the correlation between the temptation error effect and cognitive network state 1 is no longer significant ($r = -0.16$, $P = 0.12$).

Discussion

Self-control is critical for successful long-term goal attainment. Here, we use gaze pattern analysis in a self-control task and dFNC analysis of resting-state fMRI data to explore how individual differences in the ability to resist tempting distractors are related to intrinsic brain dynamics. We show that participants whose intrinsic connectivity patterns gravitate toward configurations in which salience detection systems are less strongly coupled with visual systems could resist tempting distractors more effectively.

Our results suggest that individuals whose brains spend more time in a state where SN and visual network are decoupled were less distractible by erotic pictures. Most models of self-control posit a key role for prefrontal CCNs in regulatory processes involved in overcoming the impulse to engage with salient distracting stimuli (Hare et al., 2009; Hayashi et al., 2013). The current results, in contrast, demonstrate for the first time that SN dynamic coupling tendencies

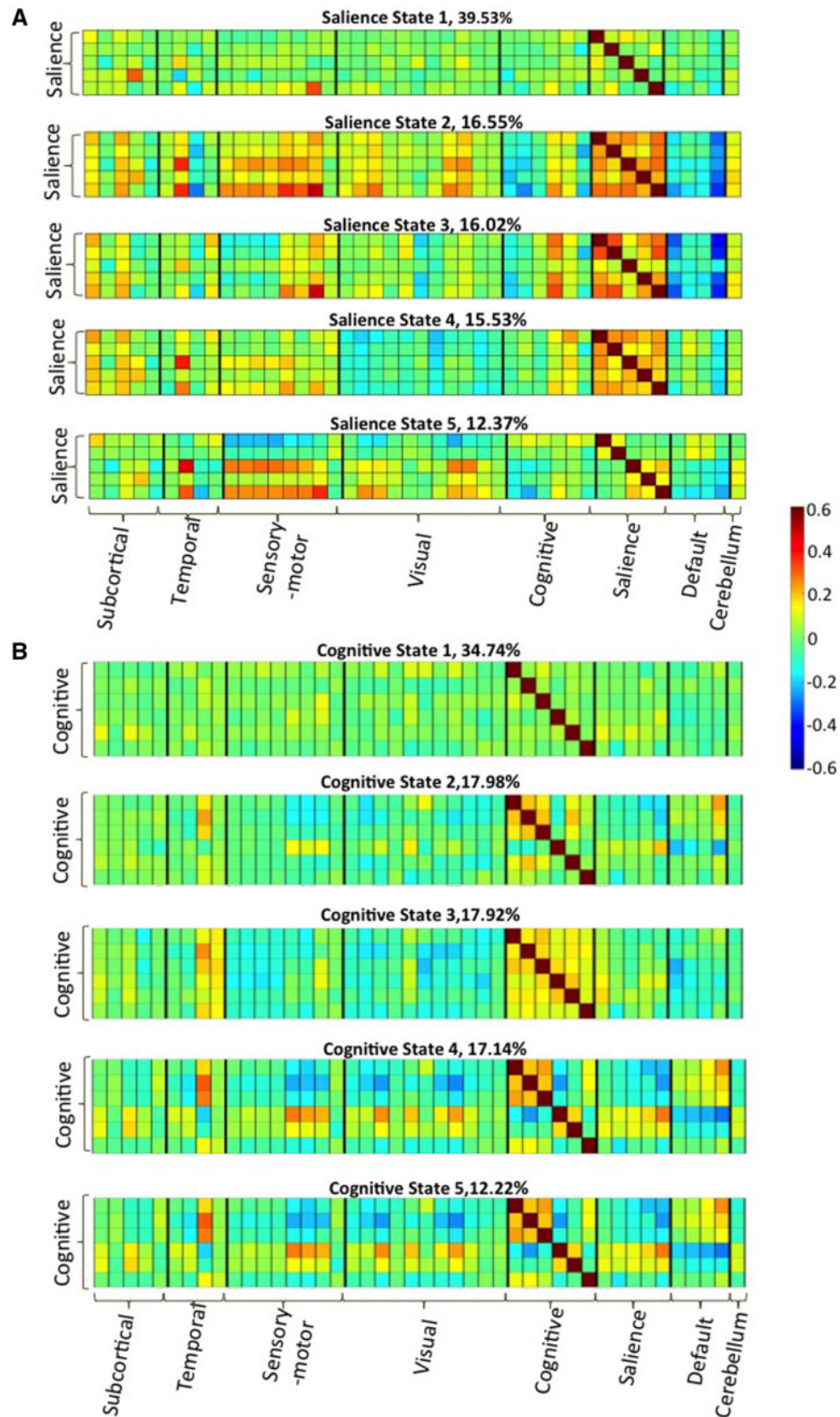


Fig. 4. Dynamic connectivity matrices. Five dynamic SN (A) and CCN states (B). States are sorted by frequency from most frequent (state 1) to the least frequent (state 5). The frequency is indicated by percent time spent in each state.

may contribute to individual differences in the ability to resist temptation.

The SN, with key nodes in insular and anterior cingulate cortices, plays a central role in detection of behaviorally relevant

stimuli and the coordination of neural resources. In particular, the dorsal anterior insular node of the SN is thought to causally influence task-positive and DMNs (Uddin et al., 2011). SN dysfunction has been linked with host of psychiatric conditions,

Table 2. Percent of time spent in each SN state

	State 1 (%)	State 2 (%)	State 3 (%)	State 4 (%)	State 5 (%)
1st analysis	39.53	16.55	16.02	15.53	12.37
2nd analysis	39.50	16.50	16.04	15.52	12.44
3rd analysis	39.53	16.54	16.03	15.53	12.36
4th analysis	39.53	16.54	16.01	15.53	12.38
5th analysis	39.53	16.55	16.02	15.53	12.37

Note: Repetition of k-means clustering reveals similar results, suggesting that the clustering is stable in this dataset.

Table 3. Percent of time spent in each CCN state

	State 1 (%)	State 2 (%)	State 3 (%)	State 4 (%)	State 5 (%)
1st analysis	34.74	17.98	17.92	17.14	12.22
2nd analysis	34.74	17.98	17.92	17.14	12.22
3rd analysis	34.55	17.97	18.21	17.13	12.15
4th analysis	34.61	17.75	18.07	17.10	12.46
5th analysis	34.74	17.98	17.92	17.14	12.22

Note: Repetition of k-means clustering reveals similar results, suggesting that the clustering is stable in this dataset.

particular those involving self-regulation and executive function deficits (Uddin, 2015). For these reasons, we predicted that individual differences in intrinsic SN dynamics may contribute to the ability to focus and maintain attention when faced with tempting distractors.

Examination of SN dynamics revealed the existence of five distinct connectivity states of this network (Figure 4). State 1, which was occupied nearly 40% of the time, was characterized by a large amount of correlations centered around zero. This is in line with previous studies (Damaraju et al., 2014; Nomi et al., 2017) which consistently show that brain states with the highest frequency of occurrence show a greater amount of correlations centered around zero compared with less frequently

occurring states. State 2 was characterized by positive correlations of the SN with the sensory motor network. Both states 2 and 3 showed positive intercorrelations within the SN and negative correlation of the salience with the DMN. State 4 also showed a negative correlation of SN with DMN and intercorrelation within SN. The most pronounced characteristic by which state 4 differed from the other states was the negative correlation of the SN and the visual network. State 4 is further characterized by medium-to-high correlations within the SN. Interestingly, in salience state 4, one node of the SN is correlated with a node from the temporal network. Specifically, the posterior insula region (see Figure 3A SN region depicted in yellow) is correlated with a node located in the temporalparietal junction (TPJ; see Figure 3A temporal network region depicted in blue). The positive insula-TPJ correlation is also visible in the whole-brain static functional connectivity correlation map (Figure 3B) and in salience state 2 and salience state 5. Thus, this connection is not unique to salience state 4. The finding of a correlation between the insula and TPJ is consistent with previous investigations of TPJ connectivity showing that regions of the TPJ are functionally connected to nodes in the insular cortex (Mars et al., 2012) and other nodes in the SN (Kucyi et al., 2012). The least frequent state 5 showed mixed positive and negative correlation with regions in the sensorimotor networks, within SN correlations centered around zero and correlation of SN with DMN centered around zero.

Examination of CCN dynamics revealed five CCN states. The most frequent CCN state (state 1) was occupied ~35 percent of the time and was characterized by a greater number of correlations centered around zero, in contrast to the other four states. This was the case for within CCN intercorrelations and correlations of the CCN with the rest of the brain.

The only significant relationship between brain network dynamics and individual differences in behavior was observed for SN state 4. Both frequency and dwell time were significantly correlated with distractibility by erotic images as measured by gaze distance from target presentation.

In a recent whole-brain dynamic functional connectivity study by Nomi et al. (2017), successful executive function was

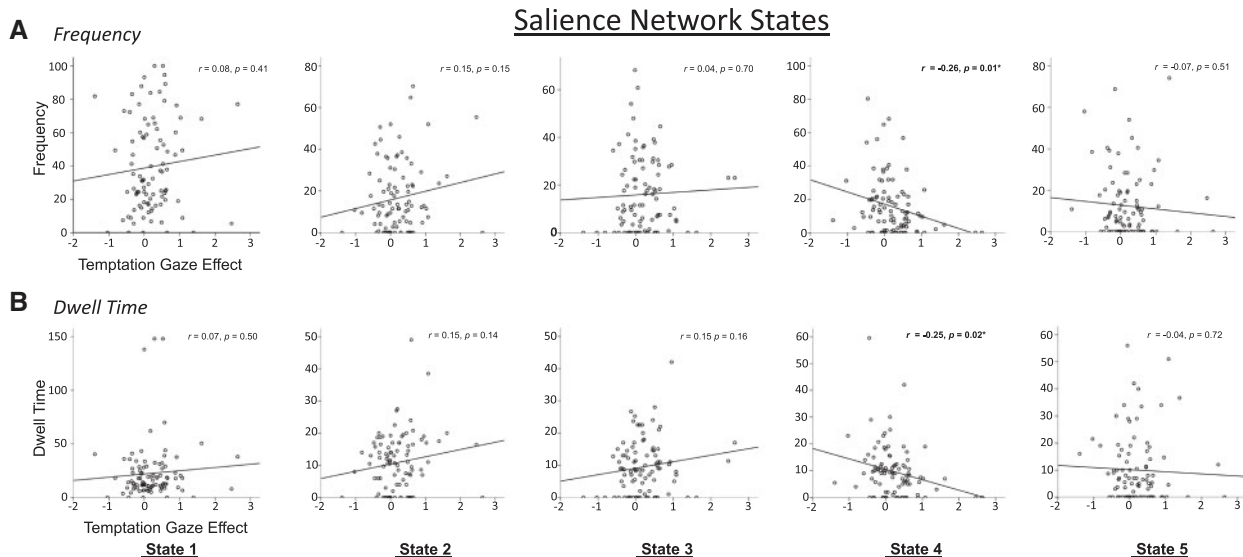


Fig. 5. Correlations between SN dynamics and behavior. (A) Frequency and (B) dwell time of the five SN states with the temptation gaze effect: the higher the temptation gaze effect, the more participants' gaze drifted from the target location in the face of tempting distractors. The asterisk (*) indicates a significant difference at $p < 0.05$.

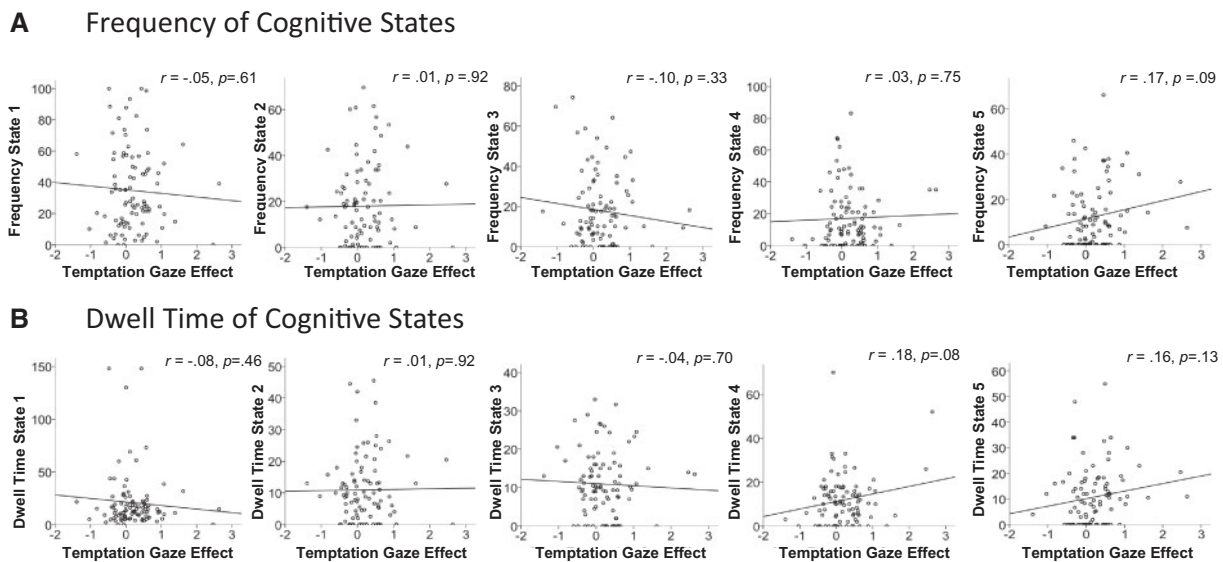


Fig. 6. Correlations between CCN dynamics and behavior. (A) Frequency and (B) dwell time of the five CCN states with the temptation gaze effect: the higher the temptation gaze effect, the higher the distractibility by erotic images.

associated with spending more time in the most frequently occurring state, whereas in our study self-control was not associated with time spent in the most frequently occurring dynamic state. These results demonstrate for the first time how highly salient distractors can interfere with top-down control processes to a greater extent in individuals who exhibit specific patterns of intrinsic functional connectivity dynamics.

The current results provide more nuanced tests of the dual-systems model, which pits cognitive control systems against ‘impulsive’ brain systems that react automatically to salient stimuli. Our separate analyses of CCN dynamics and SN dynamics indeed do not support the predictions of a traditional dual-systems approach. Instead, our findings suggest that when visual input has less access to salience detection systems, tempting erotic distractors are easier to ignore.

It is important to note that the task used in this study is a visual attention task (Steimke et al., 2016) involving inhibition of a prepotent attention allocation mechanism. SN properties might particularly explain individual differences in self-control when visual attention allocation is involved. On the other hand, individual differences in self-control tasks relying less heavily on a prepotent attention allocation mechanism may be better explained by dynamic brain states related to a reflective system involving frontoparietal control networks. Future studies should investigate individual differences in dynamic brain states supporting reflective and impulsive systems in the context of self-control tasks that involve cognitive operations other than visual attention, such as working memory updating or task switching (Miyake et al., 2000).

Taken together, our findings highlight the importance of considering ‘neural context’ in studies of brain function; the idea that the functional relevance of a brain system depends on the status of other connected areas (McIntosh, 2004; Ciric et al., 2017).

Limitations

k-means is a powerful algorithm to identify a predefined number of clusters in a dataset. However, it has also been criticized,

as the starting point of the algorithm can influence the clustering. If the number of clusters chosen does not match the dataset, the clustering can become unstable and repetition of the analysis can yield significantly different results. To address this limitation, we repeated the analysis five times. In Tables 2 and 3, the percent time spent in each state for the five analyses is presented. The divergence between analyses lies below 0.1 percent, suggesting that the divergence between analyses is minor and the k-means clustering yielded stable results in our dataset.

Recently, some critiques have attempted to identify possible shortcomings of dynamic functional connectivity analysis approaches in resting-state fMRI studies (Laumann et al., 2016). The authors argue that dynamic variations during rest are mainly explained by head motion, sampling variability and states of arousal. Thus, current measures of dynamic brain function may not actually be related to cognition. Although head motion and sleep states are certainly of concern in any fMRI study, other research demonstrates that employment of a sliding window approach, when strictly accounting for head motion through subsampling of low motion subjects (Allen et al., 2014) or scrubbing of high motion volumes (Ciric et al., 2017), and when accounting for possible states of arousal by comparing the first and second half of a resting-state scan (Allen et al., 2014; Damaraju et al., 2014), still produce results consistent with the interpretation that the brain undergoes dynamic shifts in functional connections.

With regards to statistical stationarity, recent work argues that the presence of statistical stationarity over long periods of time (e.g. averages over an entire resting-state scan) does not rule out the presence of interesting changes in covariance over shorter time periods (e.g. sliding windows) [see Miller et al. (2017) for an extensive discussion of the criticism raised by Laumann et al.]. All of these issues are also related to the use of particular approaches used to show a lack of brain dynamics due to statistically non-significant deviations from a particular ‘static’ null model. Null models used to demonstrate a lack of brain dynamics are inherently difficult to create due to the fact that brain scans are inherently dynamic, causing a considerable gulf between a simulation proposing to capture a lack of

dynamics and actual brain data (Miller et al., 2017). Additionally, many parameters of any given null model can be tuned to either show stationarity or non-stationarity, leading to difficulty in agreement regarding a proper null model of dynamic brain function. Thus, while there is still a large consensus that brain function is dynamic (Sakoglu et al., 2010; Allen et al., 2014; Damaraju et al., 2014; Jia et al., 2014; Rashid et al., 2014; Yang et al., 2014; Wilson et al., 2015; Nomi et al., 2016), there is less consensus regarding how to properly demonstrate these effects (Laumann et al., 2016).

Another limitation of the study presented here is that the behavioral task effect size is small, despite being highly significant. Additionally, frequency and dwell time of dynamic salience state 4 correlated only with eye gaze distance from target location, not with error rates. A possible explanation might be a ceiling effect for error rates, with most participants making very few errors. The eye gaze distance shows more variance and is sensitive to subtle deviations from task instruction because of temptation. Additionally, across all measures acquired during the behavioral task, gaze distance showed the highest effect size. These findings support the use of the eyetracking data as a metric of interest.

With a P-value of 0.012, the results presented here do not survive the conservative Bonferroni correction for multiple comparisons. A corrected value would be marginally significant ($P=0.06$). Therefore, the results presented here should be regarded with caution and should be replicated in future studies. With a sample size of 94, we have a relatively large sample for a combined fMRI and eyetracking study. However, as was noted by Schönbrodt and Perugini (2013) a sample size of higher than 150–250 is even more reliable for examining correlations. Future work with larger sample sizes is needed to further support the results presented here.

Finally, it should be noted that the analysis presented here is not sensitive toward general differences in reaction to erotic stimuli or general activation differences but only assesses the connectivity profile of the SN and cognitive network. Processing of erotic pictures has been associated with activity in ventral striatum, occipital cortex, hippocampus, hypothalamus, thalamus and the amygdala in univariate analyses (Stark et al., 2005; Walter et al., 2008). These regions have not been separately assessed in the study presented here.

Conclusions

Studying SN dynamics might deliver valuable insight into the origin of individual differences in self-control ability. We show that participants who spent more time in a brain network configuration in which salience detection systems are decoupled from visual systems could resist tempting distractors more effectively. This suggests that individual differences in self-control in the face of temptation might be driven in part by SN functional connectivity context.

Supplementary data

Supplementary data are available at SCAN online.

Conflict of interest. None declared.

Funding

The authors thank the Berlin School of Mind and Brain, the Humboldt University Berlin and the Collaborative Research

Centre 'Volition and Cognitive Control' (DFG grant SFB 940/1 2013), Technical University Dresden, for financially supporting the project. This work was also supported by award R01MH107549 from the National Institute of Mental Health to L.Q.U. NIH grants: 2R01EB005846, P20GM103472, and R01EB020407 as well as NSF grant #1539067 to VDC.

References

- Abou-Elseoud, A., Starck, T., Remes, J., Nikkinen, J., Tervonen, O., Kiviniemi, V. (2010). The effect of model order selection in group pica. *Human Brain Mapping*, *31*(8),1207–16.
- Allen, E.A., Erhardt, E.B., Damaraju, E., et al. (2011). A baseline for the multivariate comparison of resting-state networks. *Frontiers in Systems Neuroscience*, *5*, 2.
- Allen, E.A., Damaraju, E., Plis, S.M., Erhardt, E.B., Eichele, T., Calhoun, V.D. (2014). Tracking whole-brain connectivity dynamics in the resting state. *Cerebral Cortex*, *24*(3),663–76.
- Bechara, A. (2005). Decision making, impulse control and loss of willpower to resist drugs: a neurocognitive perspective. *Nature Neuroscience*, *8*(11),1458–63.
- Calhoun, V., Adali, T., Pearlson, G., Pekar, J. (2001). A method for making group inferences using independent component analysis of functional mri data: exploring the visual system. *Neuroimage*, *13*(6),S88.
- Calhoun, V.D., Adali, T. (2012). Multi-subject independent component analysis of fmri: a decade of intrinsic networks, default mode, and neurodiagnostic discovery. *IEEE Reviews in Biomedical Engineering*, *5*, 60–73.
- Calhoun, V.D., Miller, R., Pearlson, G., Adali, T. (2014). The chronnectome: time-varying connectivity networks as the next frontier in fmri data discovery. *Neuron*, *84*(2),262–74.
- Chang, L.J., Yarkoni, T., Khaw, M.W., Sanfey, A.G. (2013). Decoding the role of the insula in human cognition: functional parcellation and large-scale reverse inference. *Cerebral Cortex*, *23*(3),739–49.
- Ciric, R., Nomi, J.S., Uddin, L.Q., Satpute, A.B. (2017). Contextual connectivity: a framework for understanding the intrinsic dynamic architecture of large-scale functional brain networks. *Scientific Reports*, *7*(1),6537.
- Damaraju, E., Allen, E.A., Belger, A., et al. (2014). Dynamic functional connectivity analysis reveals transient states of dysconnectivity in schizophrenia. *Neuroimage Clin*, *5*, 298–308.
- Damoiseaux, J.S., Rombouts, S.A., Barkhof, F., et al. (2006). Consistent resting-state networks across healthy subjects. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(37),13848–53.
- Dubois, J., Adolphs, R. (2016). Building a science of individual differences from fmri. *Trends in Cognitive Sciences*, *20*(6),425–43.
- Erhardt, E.B., Rachakonda, S., Bedrick, E.J., Allen, E.A., Adali, T., Calhoun, V.D. (2011). Comparison of multi-subject ica methods for analysis of fmri data. *Human Brain Mapping*, *32*(12),2075–95.
- Friedman, J., Hastie, T., Tibshirani, R. (2008). Sparse inverse covariance estimation with the graphical lasso. *Biostatistics*, *9*(3),432–41.
- Fromberger, P., Jordan, K., von Herder, J., et al. (2012). Initial orienting towards sexually relevant stimuli: preliminary evidence from eye movement measures. *Archives of Sexual Behavior*, *41*(4),919–28.
- Hare, T.A., Camerer, C.F., Rangel, A. (2009). Self-control in decision-making involves modulation of the vmppfc valuation system. *Science*, *324*(5927),646–8.

- Hayashi, T., Ko, J.H., Strafella, A.P., Dagher, A. (2013). Dorsolateral prefrontal and orbitofrontal cortex interactions during self-control of cigarette craving. *Proceedings of the National Academy of Sciences of the United States of America*, **110**(11),4422–7.
- Hofmann, W., Baumeister, R.F., Forster, G., Vohs, K.D. (2012). Everyday temptations: an experience sampling study of desire, conflict, and self-control. *Journal of Personality and Social Psychology*, **102**(6),1318–35.
- Hofmann, W., Friese, M., Strack, F. (2009). Impulse and self-control from a dual-systems perspective. *Perspectives on Psychological Science*, **4**(2),162–76.
- Hofmann, W., Luhmann, M., Fisher, R.R., Vohs, K.D., Baumeister, R.F. (2014). Yes, but are they happy? Effects of trait self-control on affective well-being and life satisfaction. *Journal of Personality*, **82**(4),265–77.
- Horn, W. (1983). *L-p-s Leistungsprüfungssystem*, 2nd edn. Göttingen: Hogrefe.
- Hutchison, R.M., Womelsdorf, T., Gati, J.S., Everling, S., Menon, R.S. (2013). Resting-state networks show dynamic functional connectivity in awake humans and anesthetized macaques. *Human Brain Mapping*, **34**(9),2154–77.
- Jia, H., Hu, X., Deshpande, G. (2014). Behavioral relevance of the dynamics of the functional brain connectome. *Brain Connectivity*, **4**(9),741–59.
- Kiviniemi, V., Starck, T., Remes, J., et al. (2009). Functional segmentation of the brain cortex using high model order group pica. *Human Brain Mapping*, **30**(12),3865–86.
- Kontinen, H., Haukkala, A., Sarlio-Lähteenkorva, S., Silventoinen, K., Jousilahti, P. (2009). Eating styles, self-control and obesity indicators. The moderating role of obesity status and dieting history on restrained eating. *Appetite*, **53**(1),131–4.
- Kucyi, A., Hodaie, M., Davis, K.D. (2012). Lateralization in intrinsic functional connectivity of the temporoparietal junction with salience- and attention-related brain networks. *Journal of Neurophysiology*, **108**(12),3382–92.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N. (2008). International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-8. University of Florida, Gainesville, FL.
- Laumann, T.O., Snyder, A.Z., Mitra, A., et al. (2016). On the stability of bold fmri correlations. *Cerebral Cortex*, **27**(10),4719–32.
- Leonardi, N., Van De Ville, D. (2015). On spurious and real fluctuations of dynamic functional connectivity during rest. *Neuroimage*, **104**, 430–6.
- Ludwig, V.U., Stelzel, C., Krutlak, H., et al. (2013). Impulsivity, self-control, and hypnotic suggestibility. *Consciousness and Cognition*, **22**(2),637–53.
- Loftus, G. R., Masson, M. E. (1994). Using confidence intervals in within-subject designs. *Psychon Bull Rev*, **1**(4), 476–490.
- Mars, R.B., Sallet, J., Schuffelgen, U., Jbabdi, S., Toni, I., Rushworth, M.F. (2012). Connectivity-based subdivisions of the human right “temporoparietal junction area”: evidence for different areas participating in different cortical networks. *Cerebral Cortex*, **22**(8),1894–903.
- McClure, S.M., Bickel, W.K. (2014). A dual-systems perspective on addiction: contributions from neuroimaging and cognitive training. *Addiction Reviews*, **13**(27),62–78.
- McIntosh, A. R. (2004). Contexts and catalysts: a resolution of the localization and integration of function in the brain. *Neuroinformatics*, **2**(2), 175–182.
- Metcalf, J., Mischel, W. (1999). A hot/cool-system analysis of delay of gratification: dynamics of willpower. *Psychological Review*, **106**(1),3–19.
- Miller, R.L., Adali, T., Levin-Schwartz, Y., Calhoun, V.D. (2017). Resting-state fmri dynamics and null models: perspectives, sampling variability, and simulations. *bioRxiv*.
- Miyake, A., Friedman, N.P., Emerson, M.J., Witzki, A.H., Howerter, A., Wager, T.D. (2000). The unity and diversity of executive functions and their contributions to complex “Frontal Lobe” tasks: a latent variable analysis. *Cognitive Psychology*, **41**(1),49–100.
- Niendam, T.A., Laird, A.R., Ray, K.L., Dean, Y.M., Glahn, D.C., Carter, C.S. (2012). Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cognitive Affective & Behavioral Neuroscience*, **12**(2),241–68.
- Nomi, J.S., Farrant, K., Damaraju, E., Rachakonda, S., Calhoun, V.D., Uddin, L.Q. (2016). Dynamic functional network connectivity reveals unique and overlapping profiles of insula subdivisions. *Human Brain Mapping*, **37**(5),1770–87.
- Nomi, J.S., Vij, S.G., Dajani, D.R., et al. (2017). Chronnectomic patterns and neural flexibility underlie executive function. *Neuroimage*, **15**(147),861–71.
- Özdemir, Y., Kuzucu, Y., Ak, Ş. (2014). Depression, loneliness and internet addiction: how important is low self-control?. *Computers in Human Behavior*, **34**, 284–90.
- Paschke, L.M., Dörfel, D., Steimke, R., et al. (2016). Individual differences in self-reported self-control predict successful emotion regulation. *Social Cognitive and Affective Neuroscience*, **11**(8),1193–204.
- Power, J.D., Cohen, A.L., Nelson, S.M., et al. (2011). Functional network organization of the human brain. *Neuron*, **72**(4),665–78.
- Rashid, B., Damaraju, E., Pearlson, G.D., Calhoun, V.D. (2014). Dynamic connectivity states estimated from resting fmri identify differences among schizophrenia, bipolar disorder, and healthy control subjects. *Frontiers in Human Neuroscience*, **8**, 897.
- Reichert, T., Carpenter, C. (2004). An update on sex in magazine advertising: 1983 to 2003. *Journalism & Mass Communication Quarterly*, **81**(4),823–37.
- Sakoglu, U., Pearlson, G.D., Kiehl, K.A., Wang, Y.M., Michael, A.M., Calhoun, V.D. (2010). A method for evaluating dynamic functional network connectivity and task-modulation: application to schizophrenia. *Magnetic Resonance Materials in Physics Biology and Medicine*, **23**(5–6),351–66.
- Schönbrodt, F.D., Perugini, M. (2013). At what sample size do correlations stabilize?. *Journal of Research in Personality*, **47**(5),609–12.
- Schweitzer, J.B., Sulzer-Azaroff, B. (1995). Self-control in boys with attention-deficit hyperactivity disorder - effects of added stimulation and time. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, **36**(4),671–86.
- Seeley, W.W., Menon, V., Schatzberg, A.F., et al. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience*, **27**(9),2349–56.
- Sekutowicz, M., Schmack, K., Steimke, R., et al. (2016). Striatal activation as a neural link between cognitive and perceptual flexibility. *Neuroimage*, **141**, 393–8.
- Sennwald, V., Pool, E., Brosch, T., Delplanque, S., Bianchi-Demicheli, F., Sander, D. (2016). Emotional attention for erotic stimuli: cognitive and brain mechanisms. *Journal of Comparative Neurology*, **524**(8),1668–75.
- Shehzad, Z., Kelly, A.M.C., Reiss, P.T., et al. (2009). The resting brain: unconstrained yet reliable. *Cerebral Cortex*, **19**(10),2209–29.

- Shirer, W., Ryali, S., Rykhlevskaia, E., Menon, V., Greicius, M. (2012). Decoding subject-driven cognitive states with whole-brain connectivity patterns. *Cerebral Cortex*, *22*(1),158–65.
- Stark, R., Schienle, A., Girod, C., et al. (2005). Erotic and disgust-inducing pictures - differences in the hemodynamic responses of the brain. *Biological Psychology*, *70*(1),19–29.
- Steimke, R., Stelzel, C., Gaschler, R., et al. (2016). Decomposing self-control: individual differences in goal pursuit despite interfering aversion, temptation, and distraction. *Frontiers in Psychology*, *18*(7),382.
- Strack, F., Deutsch, R. (2004). Reflective and impulsive determinants of social behavior. *Personality and Social Psychology Review*, *8*(3),220–47.
- Uddin, L.Q. (2015). Salience processing and insular cortical function and dysfunction. *Nature Reviews Neuroscience*, *16*(1),55–61.
- Uddin, L.Q., Kinnison, J., Pessoa, L., Anderson, M.L. (2014). Beyond the tripartite cognition-emotion-interoception model of the human insular cortex. *Journal of Cognitive Neuroscience*, *26*(1),16–27.
- Uddin, L.Q., Supekar, K.S., Ryali, S., Menon, V. (2011). Dynamic reconfiguration of structural and functional connectivity across core neurocognitive brain networks with development. *Journal of Neuroscience*, *31*(50),18578–89.
- Walter, K.H., Gunstad, J., Hobfoll, S.E. (2010). Self-control predicts later symptoms of posttraumatic stress disorder. *Psychological Trauma-Theory Research Practice and Policy*, *2*(2),97–101.
- Walter, M., BERPpohl, F., Mouras, H., et al. (2008). Distinguishing specific sexual and general emotional effects in fmri-subcortical and cortical arousal during erotic picture viewing. *Neuroimage*, *40*(4),1482–94.
- Wilson, R.S., Mayhew, S.D., Rollings, D.T., et al. (2015). Influence of epoch length on measurement of dynamic functional connectivity in wakefulness and behavioural validation in sleep. *Neuroimage*, *112*, 169–79.
- Yang, Z., Craddock, R.C., Margulies, D.S., Yan, C.G., Milham, M.P. (2014). Common intrinsic connectivity states among postero-medial cortex subdivisions: insights from analysis of temporal dynamics. *Neuroimage*, *93*(Pt 1),124–37.