From noise to insight: the functional role of BOLD signal variability and aperiodic neural activity in metacontrol

Zhang, C.

Chapter 2

Resting-state BOLD signal variability is associated with individual differences in metacontrol

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Abstract

Numerous studies demonstrate that moment-to-moment neural variability is behaviorally relevant and beneficial for tasks and behaviors requiring cognitive flexibility. However, it remains unclear whether the positive effect of neural variability also holds for cognitive persistence. Moreover, different brain variability measures have been used in previous studies, yet comparisons between them are lacking. In the current study, we examined the association between resting-state BOLD signal variability and two metacontrol policies (i.e., persistence vs. flexibility). Brain variability was estimated from resting-state fMRI (rsfMRI) data using two different approaches (i.e., Standard Deviation (SD) and Mean Square Successive Difference (MSSD)) and metacontrol biases were assessed by three metacontrol-sensitive tasks. Results showed that brain variability measured by SD and MSSD was highly positively related. Critically, higher variability measured by MSSD in the attention network, parietal and frontal network, frontal and ACC network, parietal and motor network, and higher variability measured by SD in the parietal and motor network, parietal and frontal network were associated with reduced persistence (or greater flexibility) of metacontrol (i.e., larger Stroop effect or worse RAT performance). These results show that the beneficial effect of brain signal variability on cognitive control depends on the metacontrol states involved. Our study highlights the importance of temporal variability of rsfMRI activity in understanding the neural underpinnings of cognitive control.

Introduction

Neural activity is highly variable from moment to moment at every level of neural organization. Traditionally, variability of this kind is considered to be "noise" that tends to mask, overshadow, or even distort the neural signals that are assumed to represent the relevant neural processing. Accordingly, functional magnetic resonance imaging (fMRI) research typically focuses on mean activity within a voxel or brain region, but considers variance in blood oxygen level-dependent (BOLD) signal as to-be-neglected "noise" (Grady & Garrett, 2014). The same logic applies to other neuroscientific and behavioral measurements indicative of human cognitive functioning (Hommel & Colzato, 2017b).

However, accumulating evidence suggests that intra-individual variability might be functional and beneficial for cognitive performance (Garrett et al., 2010, 2011, 2013, 2018; Waschke, Kloosterman, et al., 2021), so that a better understanding of its functional role might strongly improve the diagnosis and treatment of mental disorders such as ADHD (Bluschke et al., 2017, 2021; Karalunas et al., 2014; Pertermann, Bluschke, et al., 2019). For example, higher BOLD signal variability is associated with younger age, higher accuracy, faster and more stable responses across a number of cognitive tasks spanning perception, attention, working memory, response inhibition and task switching (Armbruster-Genç et al., 2016; Garrett et al., 2010, 2011, 2013; Grady & Garrett, 2017; Guitart-Masip et al., 2016; Mennes et al., 2011; Millar et al., 2020). BOLD signal variability might reflect intrinsic properties of network organization (Garrett et al., 2018), cardiovascular and cerebrovascular factors (Tsvetanov et al., 2021), and/or general non-cognitive factors (Laumann & Snyder, 2021). Notably, previous work suggests that more pronounced brain variability might allow the brain to explore among different functional network configurations, which in turn supports cognitive flexibility – the ability to explore variable opportunities and flexibly adapt to changing circumstances (Armbruster-Genç et al., 2016; Ghosh et al., 2008; Waschke, Kloosterman, et al., 2021).

The present study was motivated by the idea that individual differences in cortical variability might be systematically related to individual cognitive-control styles, to what Hommel (2015) has called "metacontrol" (Hommel, 2015). This term refers to the control of cognitive functioning to deal with a fundamental dilemma of human cognition (Beste et al., 2018; Goschke, 2000; Goschke & Bolte, 2014): the fact that we sometimes need to be

"cognitively conservative" by sticking with our present mindset and our present goal, but to be flexible and more open to alternative goals on other occasions. Hence, people need both cognitive persistence and cognitive flexibility: while cognitive flexibility helps them to switch between alternative opportunities, intentional agents also need cognitive persistence to avoid distractions and to stick with the current goal as long as pursuing it is worthwhile (Goschke, 2003; Hommel, 2015; Hommel & Colzato, 2017c; Nijstad et al., 2010).

As Hommel's Metacontrol State Model (MSM) suggests, cognitive control emerges from the interplay of two counteracting forces or systems, one promoting cognitive persistence and the other promoting cognitive flexibility (Hommel, 2015). A metacontrol bias toward persistence is characterized by a strong top-down influence from the current goal and restricting processing to task-relevant information. In contrast, a metacontrol bias toward flexibility is characterized by a stronger bottom-up influence and openness to alternative goals and opportunities (Hommel, 2015). Truly adaptive control requires humans to find a balance between persistence and flexibility, an ability called metacontrol. Interestingly, there are systematic individual differences with respect to the metacontrol default: while some people tend to have a persistence bias, so that they perform better than others on tasks that require persistence but less well than others on tasks that require flexibility, other individuals tend to have a flexibility bias, resulting in the opposite performance profile (Hommel & Colzato, 2017c). The basic idea driving the present study was that such individual biases in metacontrol might be related to individual differences in brain variability, that is, in the individual level of the BOLD signal variability of people's brains.

We assessed our key hypothesis by testing whether an indicator of the individual degree of brain variability, our noise measure, is statistically correlated to behavior in tasks that have been shown to be diagnostic for individual biases toward metacontrol persistence or flexibility. "Noise" is defined as variability that results from random or unpredictable fluctuations and disturbances (McDonnell & Ward, 2011). We used resting-state fMRI (rsfMRI) measures as indicators of the individual variability level. RsfMRI is a spontaneous low frequency (< 0.1Hz) BOLD signal within the brain in the absence of external stimulation. Noise (at an optimal level) in rsfMRI is thought to drive the network dynamics (Deco et al., 2011; Deco, Jirsa, et al., 2009) and enables the exploration of the brain among

various functional configurations representing its dynamic repertoire (Ghosh et al., 2008). It thus seems possible that cortical noise is systematically related to metacontrol.

Various temporal variability estimation approaches for rsfMRI data have been introduced and used in previous studies (Baracchini et al., 2021; Garrett et al., 2010, 2011; Nomi et al., 2017). The simplest and most prominent measure of variability is the standard deviation (SD), which reflects the distributional width of a BOLD signal time series. The SD of a BOLD signal is related to age and cognitive performance in both younger and older adults (Garrett et al., 2010, 2011). However, SD overestimates the true dispersion when the (mean) signal varies because the calculation of SD is based on the difference between single data points and the overall mean (Mohr & Nagel, 2010). To circumvent this problem, some researchers have suggested an alternative measure – the mean squared successive difference (MSSD) (Neumann et al., 1941; Nomi et al., 2017; Samanez-Larkin et al., 2010). The MSSD captures the BOLD signal difference between successive time points and thus can adapt to changing expected (mean) signals. Although the advantages and disadvantages of different measures have been discussed in the literature (Garrett et al., 2011; Nomi et al., 2017; Samanez-Larkin et al., 2010), it is unknown whether different parameters that can be estimated on the basis of rsfMRI data reveal differences in their predictability to cognitive control. Given that we had no a-priori reason to favor one measure over another, we considered both of them, assuming that a systematic comparison would lay the grounds for choosing proper measurement approaches in future studies. Therefore, the present study employed two different brain variability measures and tested which of them, if any, would best predict performance in metacontrol-sensitive tasks.

We used two tasks in which high performance requires cognitive persistence (i.e., the Stroop task and the Remote Association Task (RAT)) and a task in which high performance depends on cognitive flexibility (i.e., the Alternate Uses Task (AUT)). Given that metacontrol biases cannot (yet) be assessed directly, we followed the previous experimental logic of comparing individual differences in tasks that rely (more) on persistence with tasks that rely (more) on flexibility (Hommel & Colzato, 2017c). Persistence is assumed to lead to a strong focus on the present goal and information strictly related to that goal, which suggests that a high degree of persistence would lead to better performance in tasks that require a strong focus on some stimuli and neglect of others. The

Stroop task (Stroop, 1935) is an excellent example for such a task. In the classical Stroop task, participants are to respond to the color of colored words while ignoring the word meaning (e.g., responding "green" to the word "RED" written in green ink (Cohen et al., 1990; Stroop, 1935; Zysset et al., 2001)). To be successful in this task, one has to process task-relevant information (i.e., color "green") and ignore task-irrelevant information (i.e., word "RED"). Individuals usually respond slower in incongruent trials (in which the color of the word and meaning are different) than in congruent trials (in which the color of the word and meaning are the same), which is known as the Stroop effect. A smaller Stroop effect can be taken to indicate a better ability in reducing cognitive conflict, which is supposed to benefit from a metacontrol bias toward persistence (e.g., Dreisbach & Goschke, 2004, who applied this logic to similar tasks). In comparison, a larger Stroop effect implies a stronger impact from task-irrelevant information, which indicates a metacontrol bias toward flexibility. As some researchers argue that reaction time (RT) difference scores are sometimes unreliable in individual differences research (Draheim et al., 2019), we also considered intra-individual variability (IIV) of Stroop performance, which can be taken to reflect the stability of metacontrol over time. More trial-to-trial variability, which was potentially induced by more frequent strategy readjustments, would indicate lesser stability of metacontrol states, i.e., higher flexibility. Conversely, less trial-to-trial variability in Stroop performance would indicate more persistence.

A second persistence-heavy task we considered was the Remote Associates Task (RAT). RAT is typically used to measure convergent thinking, which is one aspect or component of human creativity (Mednick & Mednick, 1967). It requires participants to find a single solution under highly constrained search conditions: they are presented with three words and are requested to specify the one word that can be combined with either of them (e.g., "Market", "Glue", and "Man", with the solution "Super"). While this task does require a certain degree of flexibility (in repeatedly searching through memory and considering novel possible targets), its reliance on persistence is much stronger than in tasks testing divergent thinking (Hommel, 2012; Hommel & Colzato, 2017c). Accordingly, participants with comparably better performance in the RAT would be considered to have a stronger bias toward persistence than participants with worse performance (Colzato et al., 2017).

As a flexibility-heavy task, we employed the Alternate Uses Task (AUT) (Guilford, 1967; Zhang et al., 2020). This task is traditionally used to assess divergent thinking, another component of human creativity, requiring to generate new ideas and to overcome more familiar but currently misleading ideas (Guilford, 1967; Zhang et al., 2020). As an example, a participant might be presented with the label or picture of a brick and asked to report all kinds of uses that a brick might have, including very uncommon ones. The AUT does need some degree of persistence (in keeping the original concept active to check it for possible uses), but it relies much more on flexibility (Hommel, 2012; Hommel & Colzato, 2017c). Accordingly, participants with comparably better performance in the AUT would be considered to have a stronger bias toward flexibility than participants with worse performance (Colzato et al., 2017).

In sum, the present study explored whether and how resting-state BOLD signal variability is associated with inter-individual differences in metacontrol biases toward persistence or flexibility. We examined different indicators of brain variability and three different tasks drawing on cognitive persistence or flexibility. Our main question was whether two indicators are significantly related to performance in the three behavioral tasks and whether these associations would differ between tasks tapping into persistence biases and tasks tapping into flexibility biases. We were also interested in possible differences between the two indicators in the way they are associated with such behavioral differences but had no specific hypothesis regarding such differences.

Materials and Methods

Participants

Our sample consisted of thirty-two right-handed adults (21 females; age 18 – 35 years; M = 23.81, SD = 3.53). The raw dataset, which has been reported in a previous study (Speer et al., 2022), included 40 university students reporting no history of psychiatric or neurological disorders. Six participants were excluded because of missing data for the Stroop task, RAT or AUT, or resting-state fMRI scanning; two participants were excluded because of extremely large or small Stroop effect size (i.e., exceeding group mean ± 2 standard deviations). The mean framewise displacement (FD) of all remaining participants was

smaller than 0.5 mm. The present study was approved by the Psychology Research Ethics Committee of Leiden University. The original study was approved by the Internal Review Board of the Erasmus Research Institute of Management, and all participants provided written informed consent for their participation. The current study and original study were conducted in accordance with the Declaration of Helsinki.

Behavioral assessment

Color-word matching Stroop task

An adapted version of the Stroop task (Stroop, 1935) was used. In this task, two rows of letters appeared on the screen, and participants were instructed to decide as quickly as possible whether the color of the top row letters corresponded to the color name written at the bottom row by pressing one of two buttons (see Figure 1). In congruent trials, the top row consisted of a color word ("RED," "GREEN," "BLUE," or "YELLOW") printed in a color that matches its semantic meaning (e.g., "RED" presented in red ink), and the bottom row consisted of a color word printed in white ink. For incongruent trials, the color word in the top row is printed in a color that mismatches its semantic meaning (e.g., "RED" presented in green ink). The bottom row letters were identical to the congruent condition. Participants performed 72 trials in the MRI scanner, containing 36 congruent and 36 incongruent trials. In half of the trials, the color of the top row word corresponded to the bottom color word (corresponding trials), while the color of the top row word did not correspond to the bottom word in the other half (not corresponding trials).

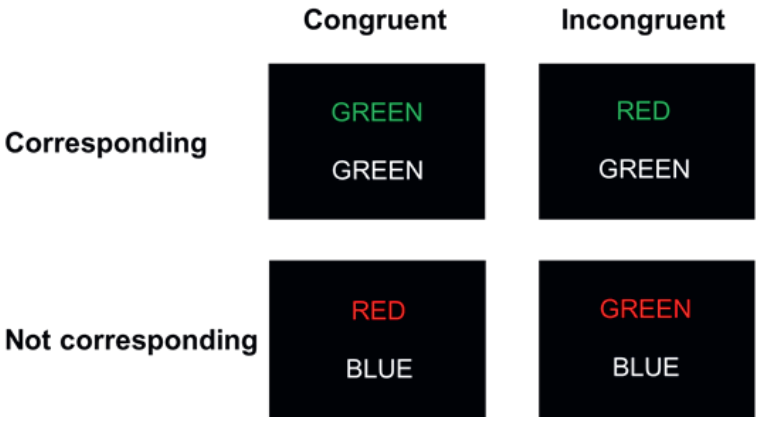

Figure 1. Examples for conditions and design of the color-word matching Stroop task. For the upper two examples, the correct answer would be "YES," and for the lower two examples, the correct answer would be "NO."

Each trial started with a fixation period of 2000 - 4000ms, followed by the stimuli presented for a maximum time of 3000ms. Afterward, feedback appeared for 1000ms. To prevent participants from focusing on the bottom word and not attending the word in the top row, the top-row word was presented 100ms before the bottom word. If no response was given within 3000ms from the onset of the stimulus presentation, an incorrect response was registered.

We calculated two parameters from the Stroop task as estimations of metacontrol biases: First, the size of Stroop effect (mean RT for incongruent trials minus mean RT for congruent trials). As we mentioned before, a smaller Stroop effect indicates a bias toward persistence, while a larger Stroop effect indicates a bias toward flexibility. Note that in our word-matching version of the Stroop task, the size of the Stroop effect may depend on the type of answer (yes or no), i.e., on the color-word correspondence (Seymour, 1969). Specifically, in non-corresponding trials (when the answer was 'NO'), the conflict generated by the Stroop effect may facilitate a 'no response', which may work against the Stroop effect. Hence, a standard Stroop effect may only occur with correspondence (when the answer was 'YES'). Therefore, we calculated the Stroop effect by subtracting the mean RT

for corresponding congruent trials from the mean RT for corresponding incongruent trials. As RT difference scores are sometimes unreliable in assessing individual differences (Draheim et al., 2019), we also calculated the intra-individual variability (IIV) of Stroop RT as a second metacontrol measure. The IIV of Stroop RT was estimated by the RT coefficient of variation across all trials (RT-CV: SD divided by mean). Greater RT-CV would reflect lesser stability of metacontrol states in the Stroop task, i.e., a bias toward flexibility. In contrast, a smaller RT-CV would be taken as a bias toward metacontrol persistence. The mean accuracy across all trials was 0.90 ($SD = 0.07$) (see the supplementary Figure S1 for the histogram). The Stroop effect and RT-CV were calculated in correct trials only. The response latency in each trial ranged from 344ms to 2995ms.

Remote Associates Task (RAT)

In each trial of this task, participants were to find a single word that can be combined with each of the three presented stimulus words (e.g., cottage, swiss, cake = "cheese"; (Mednick & Mednick, 1967). Participants had to complete 17 trials within 5 minutes. This task was completed via Qualtrics outside the scanner. To complete the RAT, participants were assumed to engage in convergent thinking, which was assumed to rely on a persistence bias (Hommel & Colzato, 2017a).

Alternate Uses Task (AUT)

Participants were presented with two everyday objects (i.e., shoe, stone) and asked to name as many possible uses (up to 6 uses) for each object as they can. This task was completed via the Qualtrics outside the scanner, and participants had 3 minutes for both objects together. Performance on AUT was scored by two independent raters from four dimensions: flexibility (number of ideas in different categories), fluency (number of uses one can think of), originality (uniqueness of responses), and elaboration (the level of details in responses). As flexibility and fluency require switching between different ideas and considering multiple solutions (Zhang et al., 2020), we used flexibility scores and fluency scores, which were averaged between two raters as metacontrol bias measures. Higher scores indicated more tendency toward flexibility, while lower scores indicated more tendency toward persistence (Zhang et al., 2020).

MRI data acquisition

MRI scanning was performed on a 3T Siemens Verio MRI system. Resting-state functional data were acquired by a T2*-weighted gradient-echo, echo-planar pulse sequence in descending interleaved order (repetition time (TR) = 2030ms, echo time (TE) = 30ms, flip angle = 75°, slice thickness = 3.0 mm, in-plane resolution = 3.0 × 3.0 mm, 64 × 64 voxels per slice). In addition to functional imaging, a T1-weighted image was acquired at the resolution of 1.0 × 0.5 × 0.5 mm for anatomical reference (192 sagittal slices, TR = 1900ms, TE = 2.26ms, flip angle = 9°).

Resting-state functional data preprocessing

Data preprocessing was performed using DPASF (http://rfmri.org/DPARSF), a Matlab toolbox for resting-state fMRI data processing & analysis (Yan et al., 2016; Yan & Zang, 2010). The first 10 volumes were discarded, and then slice-time correction and realignment were performed. Head motion was assessed by frame-wise displacement (FD) (Power et al., 2012). All participants' mean FD were smaller than 0.5 mm. Individual T1-weighted images were co-registered to the mean functional image and then segmented into gray matter, white matter (WM), and cerebrospinal fluid (CSF). Transformations from individual native space to MNI space were computed with the DARTEL tool (Ashburner, 2007), and then the functional images were normalized to MNI space with warped parameters. Lastly, all functional images were smoothed with a 6 mm full width at half maximum (FWHM) Gaussian kernel.

Group independent component analysis

As previous studies note that brain signal variability is region-specific (Armbruster-Genç et al., 2016; Mišić et al., 2010), we only selected control-related networks (i.e., independent components) which were obtained from the independent component analysis (ICA). ICA was performed using the GIFT Toolbox (https://www.nitrc.org/projects/gift) to identify temporally coherent networks that are spatially distinct. Following the processing protocol used in the previous study (Haag et al., 2015), pre-processed functional images were first intensity-normalized. Subsequently, each participant's data was reduced to 70 principal components. Then, group-level decomposition was performed using the Infomax algorithm

(Bell & Sejnowski, 1995), which resulted in 25 spatially independent components (ICs) and associated time courses. To improve the reliability of IC-decomposition, the Infomax ICA algorithm was repeated 20 times using the ICASSO toolbox (Himberg et al., 2004). Afterward, the obtained 25 ICs were visually inspected to exclude noise components. We then compared all non-noise components' spatial topology to the pre-defined resting-state network templates (Allen et al., 2011; Shirer et al., 2012). The ICs reflecting activities in the executive control network, attention network, prefrontal, and parietal regions were identified and used for further analyses. Participant-specific spatial maps and time courses were then estimated using the dual regression back-reconstruction method (Beckmann et al., 2009). We did not scale the components further due to the preprocessing step of intensity normalization, which returns back-reconstructed maps in units of percent signal change. Spatial maps for excluded components are shown in Supplementary Figure S2.

Resting-state BOLD signal variability calculation

We estimated resting-state BOLD signal variability using component-wise within-participant measures. For each component and each participant, BOLD variability was calculated. Here, we used two brain signal variability measures listed below.

First, we calculated the standard deviation (SD) of BOLD signals for each component and each participant.

As a second measure, we estimated the variability of time courses in selected ICs via mean squared successive difference (MSSD) (Baracchini et al., 2021; Nomi et al., 2017). As a non-biased estimation to SD, MSSD reflects moment-to-moment BOLD signal variability that is less sensitive to low-frequency drift (Li et al., 2017) and independent from shifts in the mean (Garrett et al., 2011). For each IC and each participant, we subtracted BOLD signals in time point t from time point t + 1, and then squared the average of all subtractions across the entire time series. (Equation (1): t and t + 1 are two successive time points belonging to the same component time course, and n is the number of time points in each component).

$$MSSD = \sqrt{\frac{\sum_{t=1}^{n-1}(x_{t+1} - x_t)^2}{n-1}} \qquad (1)$$

Statistical analysis

To examine the relationship between resting-state BOLD signal variability and individual differences in metacontrol policies, we correlated the size of the Stroop effect, Stroop RT-CV, RAT scores, AUT flexibility scores, and AUT fluency scores with brain variability estimated by SD and MSSD, respectively. As nine components were included for correlation analysis, Bonferroni correction was used to control for the increased risk of a type I error. Note that the theoretical meaning of the signs/directions of the correlations varies with task scores: Whereas higher scores in the two Stroop measures and the AUT scores imply stronger bias toward flexibility (and lower scores stronger bias toward persistence), higher scores in the RAT imply stronger bias toward persistence (and lower scores stronger bias toward flexibility).

Brain variability and RAT performance in an extended dataset

The original study collected behavioral and neural data from four separate samples (two big and two small samples) (Speer et al., 2022). Besides a big sample we reported above (referred to as Sample 1), there exists an N = 41 sample, which will be referred to as Sample 2. Sample 2 consisted of a different population, and neural data was collected in a different scanner than Sample 1. Participants in Sample 2 only completed creativity tasks, and RAT was tested by different items from those in Sample 1 (Detailed information can be found in the Supplementary Material). To test the stability of the brain-behavior correlation, we replicated the association between brain variability and RAT performance in an extended sample consisting of both Sample 1 and Sample 2 (see the Supplementary Material for details).

Results

Behavioral findings

The analysis of the Stroop data (n = 32) yielded a standard Stroop effect, with longer mean RTs in incongruent trials (1100 ms, SD = 317 ms) than in congruent trials (797 ms, SD = 234 ms), $t(31) = 4.34$, $p < 0.001$, $d = 1.09$) (see Figure 2A). Performance accuracy and speed were not significantly correlated (congruent trials: r=0.181, $p = 0.323$; incongruent trials:

r=0.260, *p* = 0.151), which rules out a speed-accuracy trade-off. Intra-individual variability of Stroop performance (RT-CV) was 0.315 ± 0.062 ms. In the RAT, participants solved 6.22 items correctly on average (*SD* = 4.09). In the AUT, inter-rater reliability was assessed by intraclass correlation coefficients (ICC), which were moderate for flexibility scores (ICC_{shoe} = 0.571, ICC_{stone} = 0.650) and for fluency scores (ICC_{shoe} = 0.705, ICC_{stone} = 0.665). The averaged AUT flexibility scores from both raters were 7.50 ± 2.04, and the averaged AUT fluency scores were 9.78 ± 2.26. Histograms displaying the distribution of above-mentioned variables are provided in supplementary Figure S3.

In order to test whether metacontrol-bias parameters extracted from various tasks and different measures were related, we applied an inter-correlation analysis between the size of the Stroop effect, RT-CV of the Stroop task, RAT scores, AUT flexibility scores, and AUT fluency scores. As displayed in Figure 2B, the size of the Stroop effect was significantly positively correlated with RT-CV (*r* = 0.403, *p* = 0.022). A highly positive correlation was also found between AUT flexibility scores and AUT fluency scores (*r* = 0.709, *p* < 0.001). Correlations between other measures were not significant. These results may indicate that participants are biased toward persistence or flexibility to a different extent, depending on the task demands.

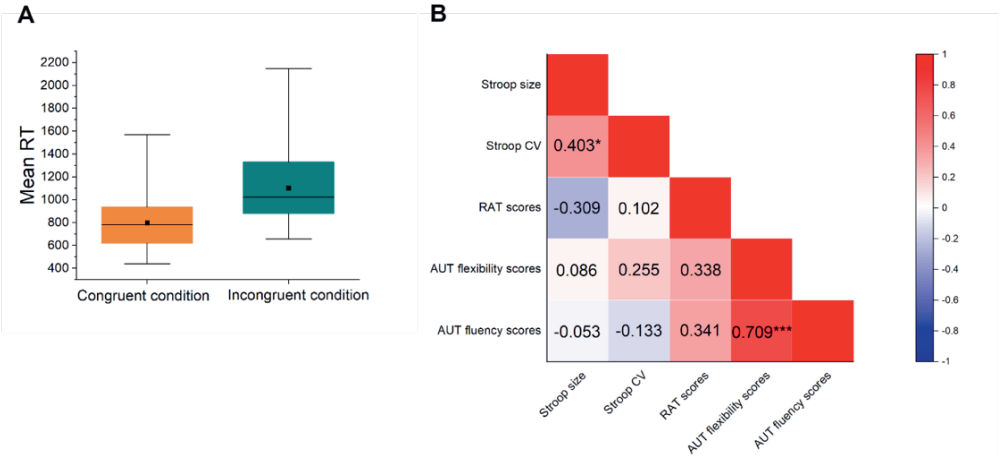

Figure 2. Statistics of mean RT in the Stroop task and inter-correlations between behavioral assessments. **(A)** mean reaction time (RT) in (corresponding) incongruent condition was larger than RT

in (corresponding) congruent condition; **(B)** inter-correlation between the size of Stroop effect, RT-CV of Stroop task, RAT scores, AUT flexibility scores, and AUT fluency scores.
Note. * = $p < 0.05$, *** = $p < 0.001$

Resting-state independent components findings

The spatial maps at the threshold of $Z > 1.0$ and the time courses of our selected ICs are shown in Figure 3. IC1 and IC4 mainly reflect activities in bilateral precuneus, superior and inferior parietal regions, within the parietal cortex. IC2 includes bilateral inferior prefrontal gyrus, middle temporal gyrus, and angular gyrus. Bilateral inferior parietal regions, postcentral and precentral areas are involved in IC3, which was defined as a parietal and motor network. IC5 reflects the left-sided executive control network, including the left prefrontal and parietal cortex, while IC7 represents the right executive control network (Shirer et al., 2012). IC6 mainly includes the bilateral middle part of the orbital frontal gyrus and precuneus, which was defined as the frontal and parietal network. IC8 represents activity in the anterior cingulate cortex, the prefrontal cortex, and the bilateral insular, which was denoted as the attention network (Allen et al., 2011). IC9 mainly reflects activity in the prefrontal cortex and extends to the anterior cingulate cortex.

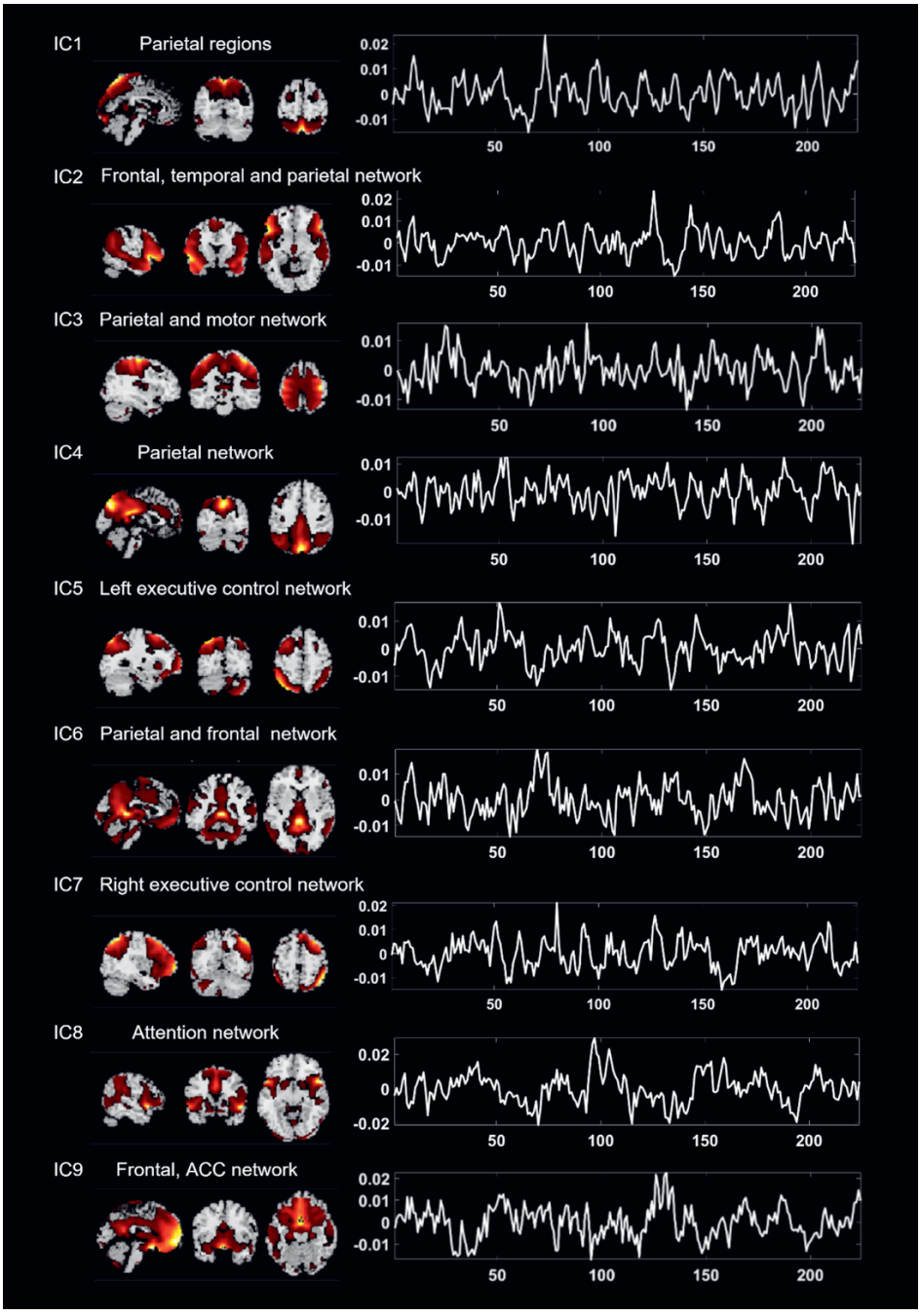

Figure 3. Spatial maps (*Z*-threshold > 1.0, in the left panel) and time series (in the right panel) for selected independent components of the mean for all participants.

To assess whether brain variability correlated between different measures, we tested the Pearson correlations between brain variability measured by SD and MSSD. Results showed that SD and MSSD of BOLD signals were highly positively correlated for all ICs (see Table 1 for details), suggesting that these two approaches are consistent in assessing the temporal variability of rsfMRI data.

Table 1. *Pearson correlations between brain variability measured by SD and MSSD.*

ICs	Correlation between SD and MSSD	
	r	p
IC1	**0,742**	**< .0001**
IC2	**0,551**	**0,0011**
IC3	**0,829**	**< .0001**
IC4	**0,731**	**< .0001**
IC5	**0,629**	**0,0001**
IC6	**0,710**	**< .0001**
IC7	**0,623**	**0,0001**
IC8	**0,523**	**0,0021**
IC9	**0,586**	**0,0004**

Note. IC = Independent component, SD = standard deviation, MSSD = mean squared successive difference.

Resting-state BOLD variability and individual difference in metacontrol policies

The analysis of the SD measure revealed that the SD of all selected components was positively correlated with the size of the Stroop effect. A pattern of positive correlations was also obtained between the MSSD of all components and the size of the Stroop effect. A close to significance positive correlation was found between MSSD of IC8 (i.e., attention network) and the size of the Stroop effect ($r = 0.468$, $p_{\text{uncorrected}} = 0.007$, $p_{\text{corrected}} = 0.062$) (Figure 4;

see Table 2 for details). We performed a supplementary analysis in which we included two participants who were excluded due to the extreme value in the Stroop effect. Results showed that the association between MSSD of IC8 and Stroop effect size is not significant (see the supplementary Figure S4 for an updated scatterplot). No significant correlations were found between RT-CV of Stroop task and brain variability as measured by SD or MSSD.

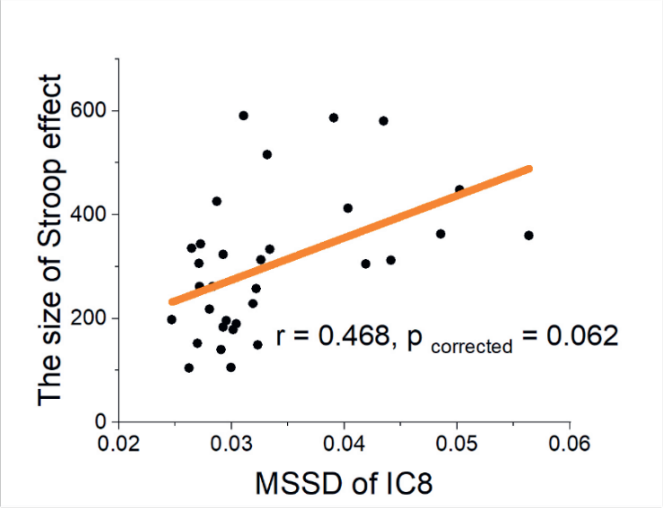

Figure 4. The correlation between the size of the Stroop effect and brain variability of the attention network (i.e., IC8) was close to significance. The higher the brain variability of IC8 estimated by MSSD, the larger the size of the Stroop effect.

Regarding RAT performance, the SD of all ICs revealed negative correlations. SD of IC3 (i.e., parietal and motor network) and IC6 (i.e., parietal and frontal network) was significantly negatively correlated with RAT performance (IC3: r = -0.505, $p_{\text{uncorrected}}$ = 0.003, $p_{\text{corrected}} < 0.05$; IC6: r = -0.508, $p_{\text{uncorrected}}$ = 0.003, $p_{\text{corrected}} < 0.05$) (see Figure 5A and 5B). A similar pattern of negative correlations was displayed between the MSSD of all components and RAT scores. Most significant negative correlations were found between MSSD of IC6 (i.e., parietal and frontal network), IC9 (i.e., frontal and ACC network) and RAT performance (IC6: r = -0.543, $p_{\text{uncorrected}}$ = 0.001, $p_{\text{corrected}} < 0.05$; IC9: r = -0.510, $p_{\text{uncorrected}}$ = 0.003, $p_{\text{corrected}} < 0.05$) (see Figure 5C and 5D). We found a close to significant negative correlation between the MSSD of IC3 and RAT scores (r = -0.470, $p_{\text{uncorrected}}$ =

0.007, $p_{corrected} = 0.059$) (see Figure 5E). These results were replicated in the supplementary analysis in which two excluded participants were included (see supplementary Figure S5 for details).

AUT flexibility and fluency scores were not significantly related to brain variability.

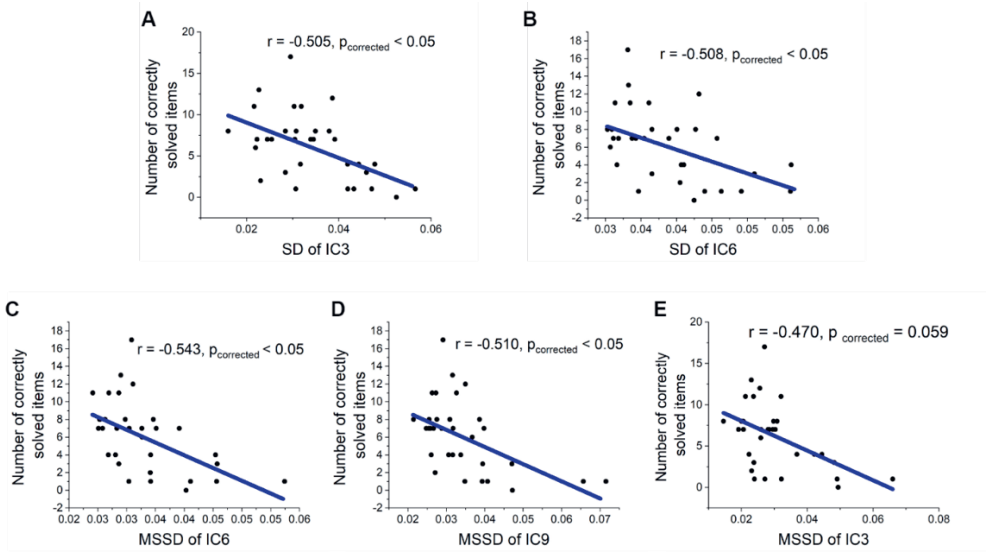

Figure 5. RAT performance was significantly (or, in the case of e, close to significantly) negatively correlated with brain variability of the parietal and motor network (i.e., IC3), parietal and frontal network (i.e., IC6), frontal and ACC network (i.e., IC9). Brain variability was calculated using SD in **(A)** and **(B)**; brain variability was measured by MSSD in **(C), (D),** and **(E)**.

Table 2. *Correlations between brain variability measured by SD, MSSD, and metacontrol policies measured by the size of Stroop effect, IIV of Stroop performance (RT-CV), RAT scores, AUT flexibility scores, and AUT fluency scores.*

Brain variability measures	ICs	Size of Stroop effect			RT-CV of Stroop task			RAT scores			AUT flexibility scores			AUT fluency scores		
		r	$p_{uncorrected}$	$p_{corrected}$	r	$p_{uncorrected}$	$p_{corrected}$	r	$p_{uncorrected}$	$p_{corrected}$	r	$p_{uncorrected}$	$p_{corrected}$	r	$p_{uncorrected}$	$p_{corrected}$
SD	IC1	0.117	0.523	1.000	0.030	0.870	1.000	-0.117	0.522	1.000	0.024	0.898	1.000	0.089	0.627	1.000
	IC2	0.260	0.150	1.000	0.003	0.986	1.000	-0.305	0.089	0.805	0.135	0.461	1.000	0.141	0.441	1.000
	IC3	0.379	0.032	0.292	0.123	0.502	1.000	**-0.505**	**0.003**	**0.029**	-0.086	0.639	1.000	-0.054	0.768	1.000
	IC4	0.422	0.016	0.145	0.175	0.337	1.000	-0.146	0.424	1.000	0.027	0.883	1.000	0.014	0.937	1.000
	IC5	0.258	0.154	1.000	-0.009	0.962	1.000	-0.223	0.221	1.000	0.071	0.701	1.000	0.226	0.213	1.000
	IC6	0.319	0.076	0.680	-0.128	0.487	1.000	**-0.508**	**0.003**	**0.027**	-0.187	0.307	1.000	-0.063	0.730	1.000
	IC7	0.116	0.529	1.000	0.000	0.998	1.000	-0.173	0.343	1.000	0.092	0.617	1.000	0.125	0.495	1.000
	IC8	0.339	0.057	0.517	0.215	0.238	1.000	-0.194	0.286	1.000	0.216	0.236	1.000	0.030	0.870	1.000
	IC9	0.334	0.062	0.554	0.286	0.113	1.000	-0.440	0.012	0.105	0.034	0.852	1.000	-0.006	0.974	1.000
MSSD	IC1	0.325	0.070	0.629	-0.005	0.978	1.000	-0.321	0.074	0.663	-0.108	0.558	1.000	0.031	0.864	1.000
	IC2	0.406	0.021	0.192	-0.023	0.902	1.000	-0.376	0.034	0.306	-0.019	0.918	1.000	0.160	0.380	1.000
	IC3	0.426	0.015	0.135	0.074	0.686	1.000	**-0.470**	**0.007**	**0.059**	-0.141	0.443	1.000	-0.168	0.357	1.000
	IC4	0.315	0.079	0.710	0.024	0.896	1.000	-0.178	0.330	1.000	-0.217	0.233	1.000	0.022	0.907	1.000
	IC5	0.397	0.024	0.220	0.044	0.811	1.000	-0.279	0.122	1.000	0.038	0.837	1.000	0.115	0.531	1.000
	IC6	0.346	0.052	0.470	-0.096	0.603	1.000	**-0.543**	**0.001**	**0.012**	-0.128	0.486	1.000	0.040	0.827	1.000
	IC7	0.344	0.054	0.487	0.016	0.929	1.000	-0.204	0.263	1.000	0.039	0.831	1.000	0.193	0.289	1.000
	IC8	**0.468**	**0.007**	**0.062**	0.233	0.200	1.000	-0.365	0.040	0.358	-0.070	0.702	1.000	-0.084	0.649	1.000
	IC9	0.433	0.013	0.119	0.046	0.801	1.000	**-0.510**	**0.003**	**0.026**	-0.066	0.720	1.000	0.005	0.979	1.000

Note. IC = Independent component, SD = standard deviation, MSSD = mean squared successive difference, RT-CV = coefficient of variation in reaction time, RAT = remote association task, AUT = alternative uses task, $P_{corrected}$ = Bonferroni corrected p value.

Resting-state BOLD variability and RAT performance in the extended dataset

With 69 participants, we obtained 11 ICs that reflect activities in control-related brain networks (see supplementary Figure S7 for details). The temporal variability measured by SD and MSSD was highly positively correlated (see supplementary Table S1). SD and MSSD of all selected ICs revealed negative correlations with the RAT score. We found a significant negative correlation between the MSSD of frontal motor regions (i.e., new IC3, see Figure S7 for details) and the RAT score (r = -0.350, $p_{\text{uncorrected}}$ = 0.003, $p_{\text{corrected}} < 0.05$) (see Figure S8 and Table S2). No significant association was detected between brain variability of other ICs and RAT scores. AUT flexibility scores and AUT fluency scores were not significantly correlated with the SD or MSSD of selected ICs.

Discussion

The present study explored the relationship between the individual's resting-state BOLD signal variability and individual differences in metacontrol biases toward persistence or flexibility. Two BOLD signal variability measures were compared. We found that resting-state BOLD signal variability measured by SD and MSSD was highly positively correlated. Notably, our results suggest that higher levels of resting-state BOLD variability measured by MSSD in the attention network, parietal and frontal network, frontal and ACC network, parietal and motor network, and variability measured by SD in the parietal and motor network, parietal and frontal network were associated with lesser persistence (or more flexibility) (denoted by larger Stroop effect or worse RAT performance) than lower levels of brain variability in these networks.

Correlations between two brain variability measures suggest that resting-state BOLD signal variability estimated by SD and MSSD is highly correlated. The high correlation between the SD measure and the MSSD measure is consistent with findings from Garrett and colleagues (Garrett et al., 2011). Although SD as a measure of brain variability has been criticized for its dependence on shifts in the mean and MSSD was recommended to prevent this problem, our findings where MSSD and SD show highly consistent results suggest that SD is an appropriate variability measure in resting-state fMRI data where (mean) signals are relatively constant.

We found that brain signal variability measured by SD and MSSD in a range of resting-state networks was positively associated with metacontrol biases toward flexibility but negatively associated with metacontrol biases toward persistence. Our findings extend previous knowledge of the relationship between brain variability and human behavior in two ways:

First, resting-state BOLD signal variability is meaningful and can tentatively be taken as a neural marker of metacontrol biases toward persistence or flexibility. Previous investigations have identified the *on-task* brain variability, which varies between cognitive demands (Garrett et al., 2013), attentional states (Grady & Garrett, 2017), task conditions (Mišić et al., 2010), and perceptual input (Garrett et al., 2020). We suggest that *off-task* variability can also be used as a trait-like neural marker of the individual metacontrol bias and, thus, as a predictor of individual cognitive control performance.

Second, although numerous studies demonstrate general positive effects of higher brain variability on cognitive performance (Garrett et al., 2010, 2011, 2013, 2014, 2020; Guitart-Masip et al., 2016; Waschke, Kloosterman, et al., 2021), our results suggest that the beneficial effect of brain variability may depend on cognitive demands and metacontrol states involved. Our findings are in line with the previous task-based fMRI study suggesting that higher brain signal variability levels are beneficial for task switching but detrimental for distractor inhibition (Armbruster-Genç et al., 2016). Hence, brain variability should not be considered as a general performance booster, but as a factor that can be beneficial for some tasks but impair performance in others. How might signal variability in the brain translate into metacontrol biases toward persistence or flexibility? Researchers have proposed that dopamine (DA) and inter-individual differences in DA levels and/or the dynamics of these levels over time are promising candidates for linking characteristics of neural processing, like differences in neural variability, to behavior (Bäckman et al., 2010; Cools & D'Esposito, 2011; Cools Roshan, 2011; Waschke, Kloosterman, et al., 2021) and some evidence suggests that dopaminergic (or catecholamine system activity) is associated with metacontrol (Pertermann, Mückschel, et al., 2019; Schlüter et al., 2019; Zink et al., 2018, 2019).

According to the computational model proposed by Durstewitz and Seamans (Durstewitz & Seamans, 2008), a D2-dominated state related to a low energy barrier among activity states would allow easier and faster transition between different cortical network

states (Armbruster-Genç et al., 2016). This D2-dominated state facilitates switching among representations at the behavioral level and supports metacontrol biases toward flexibility (Durstewitz & Seamans, 2008; Hommel & Colzato, 2017c). Conversely, D1-dominated states are associated with a high energy barrier, leading to more stable brain activity patterns and a more difficult transition between different network states (Armbruster-Genç et al., 2016; Durstewitz & Seamans, 2008).

At the same time, this D1-dominated state boosts the robustness of items in working memory and promotes metacontrol biases toward persistence (Durstewitz & Seamans, 2008; Hommel & Colzato, 2017c). Evidence from simulation research suggests that dynamics of the brain's intrinsic properties may help keep the system in a state where different subnetworks compete with each other (Deco, Jirsa, et al., 2009). Such an active resting-state (at an optimal level) can be sensitive to external signals, which can trigger brain activity during different tasks, thus supporting behavioral exploring and switching. In contrast, sensitivity to external stimuli makes people more likely to be distracted by task-irrelevant stimuli.

We found that resting-state BOLD variability of the parietal and motor network (IC3), parietal and frontal network (IC6), attention network (IC8), and frontal and ACC network (IC9) was positively associated with metacontrol biases toward flexibility but negatively associated with metacontrol biases toward persistence. Previous work suggests that distractor inhibition and task switching rely on a shared frontoparietal network, and brain activity varies depending on the exact cognitive processing involved (Armbruster et al., 2012). As a control network, the frontoparietal network plays a crucial role in task adaptation, implementation, and flexible modulation of cognitive control (Marek & Dosenbach, 2018). Moreover, the frontoparietal network is a globally functional hub that flexibly interacts with other brain networks. Higher variability in frontal and parietal regions may indicate more dynamic connectivity between brain networks with the frontoparietal network as the hub, and thus supports the flexibility of metacontrol, but hampers the persistence of metacontrol (Marek et al., 2015; Power et al., 2013). The attention network, which mainly includes ACC, prefrontal cortex, and insular, has been shown to be involved in sustained focus on task-relevant information and conflict resolution (Banich et al., 2000;

Gruber et al., 2002). A variable attention network may reveal flexible attention resource allocation, which is beneficial for flexibility but detrimental for persistence.

Whereas the analyses of the Stroop and the RAT data provide a rather consistent picture, this is not the case with respect to the AUT findings. On the one hand, previous studies have rarely found RAT performance to be an exact mirror image of AUT performance; rather, various manipulations affected either only one of the two tasks or at least one of the more than the other (Colzato et al., 2012, 2017). This suggests that both tasks are likely to capture aspects of metacontrol persistence and flexibility, but they can hardly be viewed as a direct measure of the respective metacontrol states. It is also likely that they differ in sensitivity, presumably depending on the experimental setting. Hence, it does not seem to be odd per se that only one of the two creativity tasks showed systematic effects. On the other hand, however, it is also possible that our particular assessment of divergent thinking was suboptimal. Due to the time limit in Qualtrics, our AUT task only allowed up to 6 responses within a short time duration for each item. This might have created ceiling effects, so that especially the fluency and flexibility scores were likely to be less sensitive to interindividual differences than the standard versions of the AUT. This must have reduced the variability of the data, which in turn could have worked against finding significant correlations. Accordingly, we are reluctant to draw strong conclusions from the absence of correlations related to the AUT.

Another potential limitation of our explorative study is the sample size, which in turn resulted from our use of already collected data. Larger sample sizes would be beneficial for probing brain-behavior relationships. Accordingly, we consider the outcomes of the present study as preliminary and in need of replication, but at the same time encouraging for further studies on the relationship between brain variability and metacontrol policies.

To conclude, we aimed to explore the relationship between resting-state BOLD signal variability and metacontrol policies and compared two previously used brain variability estimation metrics. We demonstrated that temporal brain variability during resting-state is associated with metacontrol biases toward persistence or flexibility, highlighting the importance of temporal variability of brain activity in understanding the neural underpinnings of cognitive control. Moreover, we found that BOLD signal variability is antagonistically related to metacontrol biases toward persistence or flexibility, suggesting

that the beneficial effect of brain variability on cognitive control may depend on the metacontrol modes involved. At last, the SD and MSSD indices of rsfMRI brain variability provide consistent pictures for predicting behavioral cognitive control.

Supplementary Information

The distribution of accuracy on the color-word matching Stroop task

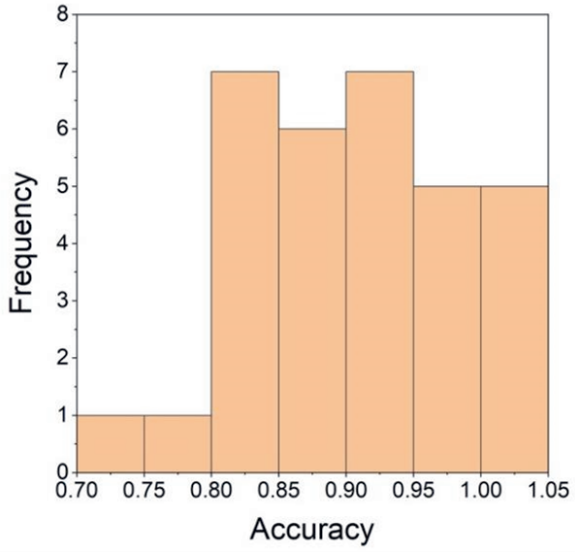

Figure S1. The histogram of the accuracy on the Stroop task. The accuracy was estimated based on the average of all trials in the Stroop task.

Excluded independent components in the group independent component analysis

Spatial maps for 16 excluded independent components (ICs) are shown in Figure S2.

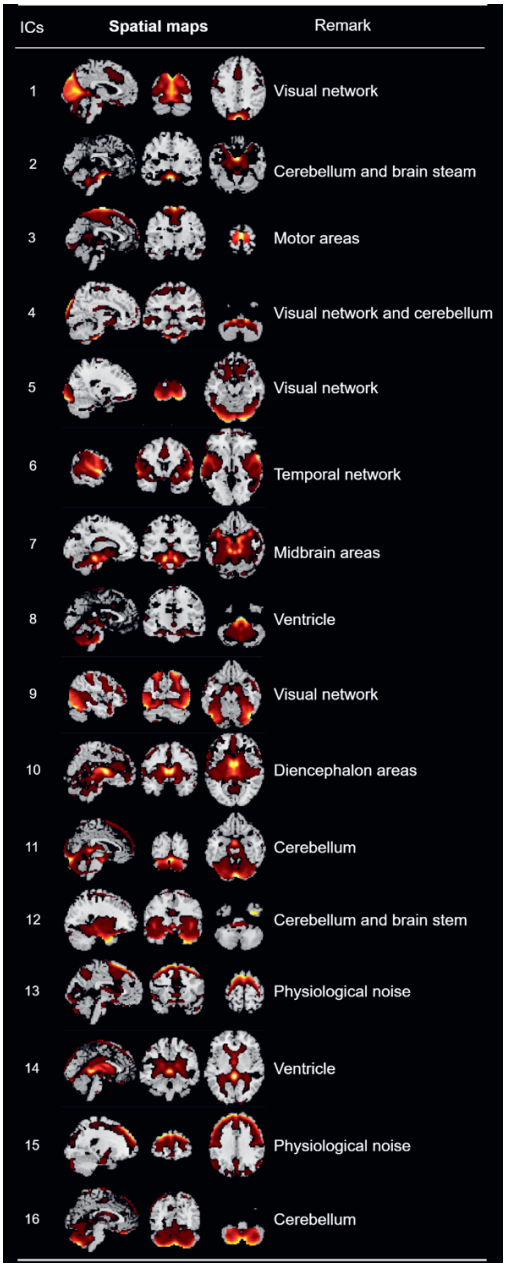

Figure S2. Spatial maps (Z-threshold > 0.1) for excluded independent components.

The distribution of the RT-Stroop effect, RT-CV of Stroop performance, RAT scores, AUT fluency scores, and AUT flexibility scores

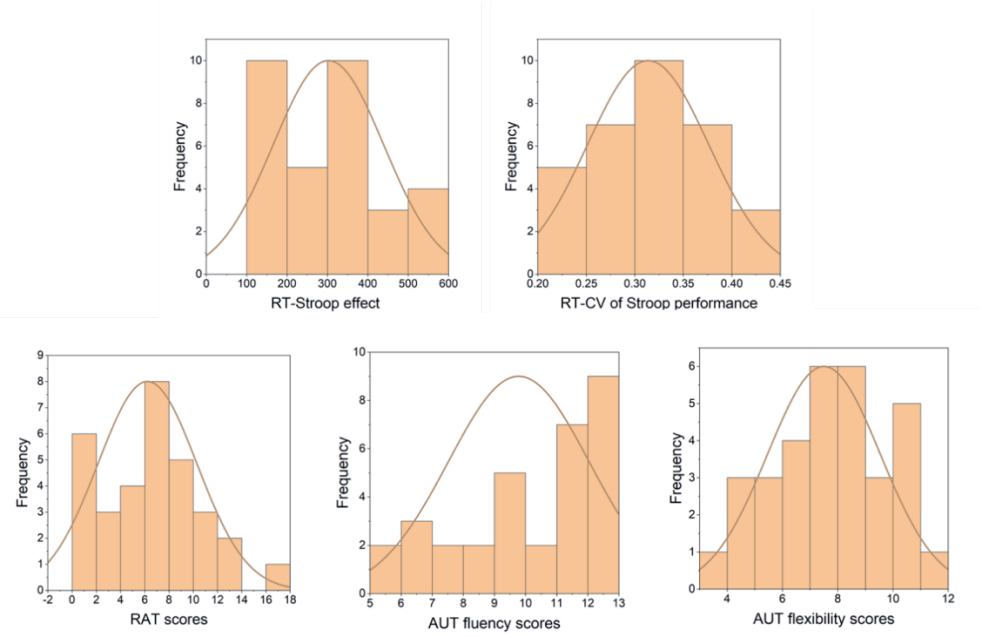

Figure S3. Histograms of the RT-Stroop effect, RT-CV of Stroop performance, RAT scores, AUT fluency scores, and AUT flexibility scores.

The relationship between resting-state BOLD signal variability and metacontrol when two participants with extreme Stroop effect are included

Two participants were identified as outliers in the Stroop task. If these participants are included, we didn't find a significant correlation between BOLD signal variability and the Stroop effect or Stroop RT-CV. Figure S4 displayed an updated scatterplot of the relation between the MSSD of IC8 and the size of the Stroop effect.

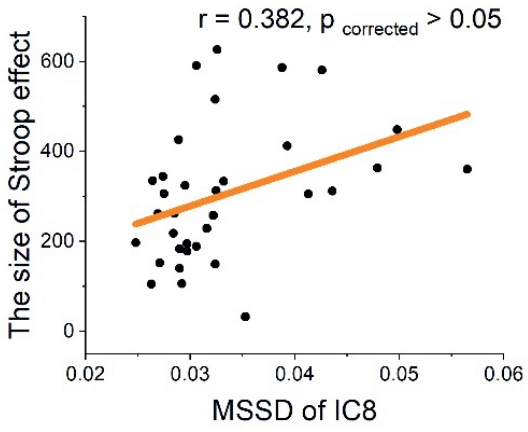

Figure S4. The correlation between the size of the Stroop effect and brain variability of the attention network (i.e., IC8) was not significant.

The association between brain variability and RAT performance almost remains the same (see Figure S5). More specifically, the SD of IC3 (i.e., parietal and motor network) and IC6 (i.e., parietal and frontal network) was significantly negatively correlated with the RAT performance (IC3: $r = -0.569$, $p_{\text{uncorrected}} < 0.001$, $p_{\text{corrected}} < 0.05$; IC6: $r = -0.484$, $p_{\text{uncorrected}} = 0.004$, $p_{\text{corrected}} < 0.05$) (see Figure S5a and S5b). The MSSD of IC3, IC6 and IC9 was significantly negatively correlated with the RAT performance (IC3: $r = -0.476$, $p_{\text{uncorrected}} = 0.004$, $p_{\text{corrected}} < 0.05$; IC6: $r = -0.515$, $p_{\text{uncorrected}} = 0.002$, $p_{\text{corrected}} < 0.05$; IC9: $r = -0.522$, $p_{\text{uncorrected}} = 0.002$, $p_{\text{corrected}} < 0.05$) (see Figure S5c, S5d, and S5e). AUT flexibility and fluency scores were not significantly related to brain variability.

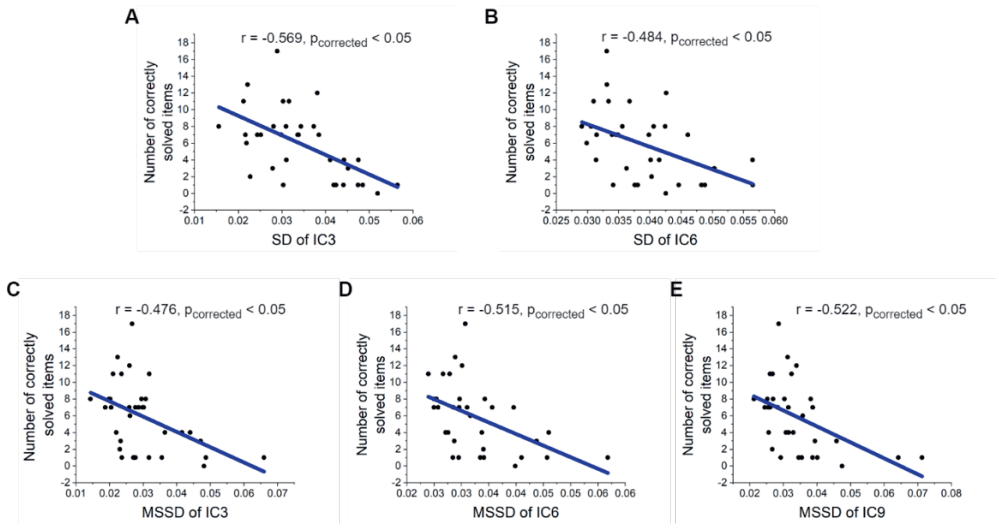

Figure S5. RAT performance was significantly negatively correlated with brain variability of the parietal and motor network (i.e., IC3), parietal and frontal network (i.e., IC6), frontal and ACC network (i.e., IC9). Brain variability was calculated using SD in **(A)** and **(B)**; brain variability was measured by MSSD in **(C)**, **(D),** and **(E)**.

Information about the Sample 2 (i.e., N = 41 sample)

Participants

The N=41 sample consisted of a general population from a different city and neural data was collected in a different scanner than Sample 1 (Speer et al., 2020). Four participants were excluded as they did not complete the RAT, AUT, or mean FD > 0.5mm. Thirty-seven participants were remaining for further analyses (N = 37, 21 females; age 18 - 43 years, M = 24.76, SD = 5.63).

Remote Associates Task (RAT)

Participants were required to complete a Dutch version of RAT (Akbari Chermahini et al., 2012). RAT items in this sample were different from those in the Sample 1. Participants had to complete 17 trials within 5 minutes. This task was completed via Qualtrics outside the scanner.

Alternate Uses Task (AUT)

Participants were asked to complete an AUT task which is similar to that reported in the main text.

MRI data acquisition

The functional magnetic resonance images were collected on a 3T Phillips Achieva MRI system. Resting-state functional data were acquired by a T2∗-weighted gradient-echo, echo-planar pulse sequence in descending interleaved order (TR = 2000ms; TE = 27ms; flip angle = 76°; slice thickness = 3.0mm; in-plane resolution = 3.0 × 3.0 mm; 64 × 64 voxels per slice,). A T1-weighted scan was acquired using 3D fast field echo (TR = 82ms; TE = 38ms; flip angle = 8°; FOV = 240 × 188 mm; 220 slices acquired using single-shot ascending slice order and a voxel size of 1 × 1 × 1 mm). The functional scans were acquired for 8 min.

Resting-state functional data preprocessing

The first 6 volumes were discarded to eliminate T1-equilibration artifacts from the time series. Subsequently, preprocessing was performed using the CONN preprocessing pipeline in MATLAB. Functional images were motion-corrected using the realign & unwrap procedure followed by slice-timing correction. Functional images were then co-registered to the T1 image. Both the functional and the structural data were normalized into standard MNI space. Functional data were then smoothed with a Gaussian kernel of 6 mm full width half maximum.

Resting-state BOLD signal variability and metacontrol in the extended dataset

Participants

The extended sample was comprised of 69 healthy adults (42 females; age 18 – 43 years; *M* = 24.32, *SD* = 4.78). 32 of them were from Sample 1 and 37 of them were from Sample 2.

Group independent component analysis

Preprocessed functional images from all 69 participants were entered into the GIFT toolbox for the independent component analysis. We used the same ICA analysis method as described in the main paper.

Resting-state BOLD signal variability calculation

For each component and each participant, the SD and MSSD of the BOLD signal were calculated. We then correlated the RAT score with brain variability estimated by SD and MSSD, respectively. Bonferroni correction was used to reduce the chances of type I errors.

Results

Behavioral findings

In the RAT, participants solved 5.66 items correctly on average (SD = 3.31). The averaged AUT flexibility scores were 7.31 ± 1.82, and averaged AUT fluency scores were 9.64 ± 2.21. Consistent with our findings in Sample 1, AUT flexibility scores and AUT fluency scores were highly positively correlated ($r = 0.731$, $p < 0.001$), while correlations between RAT scores and two AUT scores were not significant (see Figure S6).

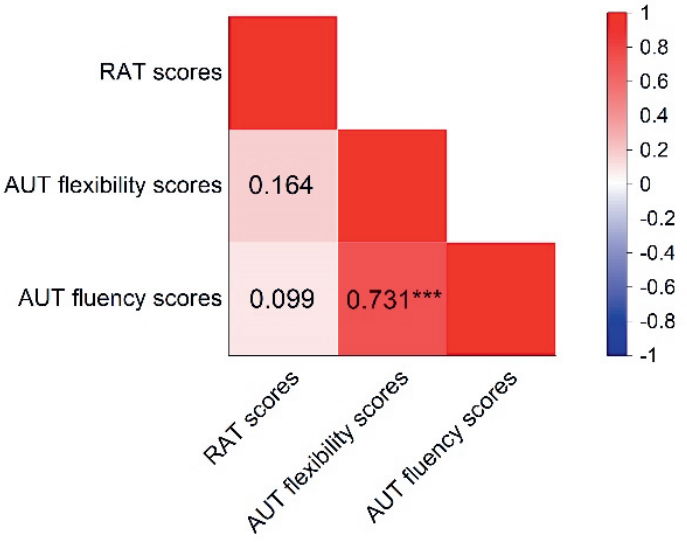

Figure S6. Inter-correlation between RAT scores, AUT flexibility scores, and AUT fluency scores.
Note. * = p < 0.05, *** = p < 0.001

Resting-state independent components findings

11 ICs which reflect the activity in the "executive control network", the "frontal network" and the "parietal network" were chosen for the brain variability calculation. The spatial maps at the threshold of Z > 1.0 and the time courses of our selected ICs are shown in Figure S7.

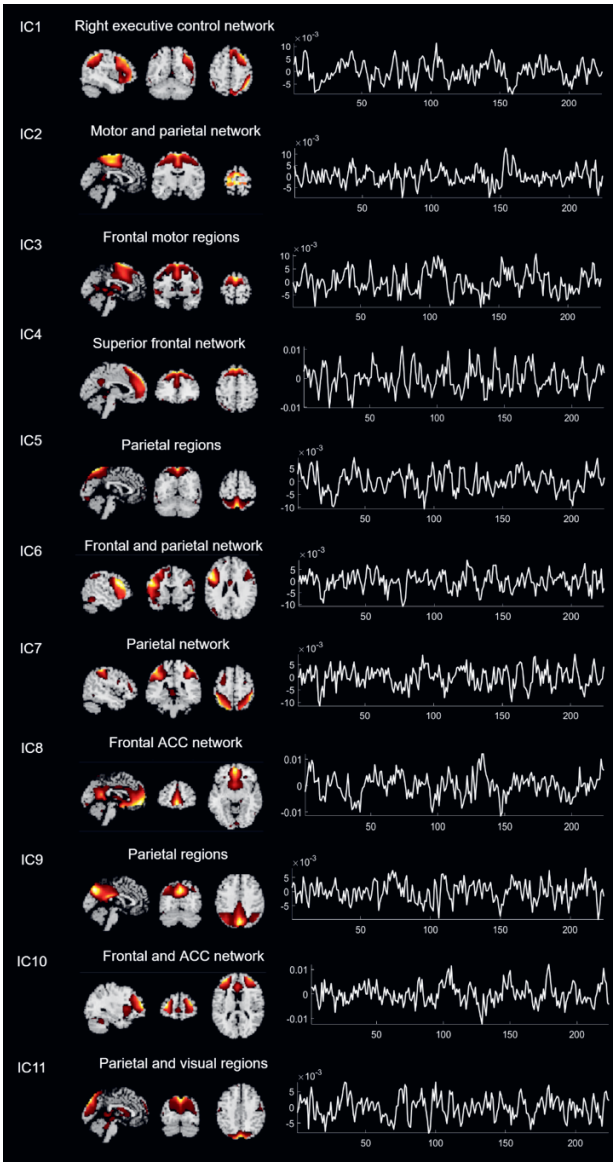

Figure S7. Spatial maps (*Z*-threshold > 1.0, in the left panel) and time series (in the right panel) for selected independent components of the mean for all participants.

Correlation analyses showed that SD and MSSD of BOLD signals were highly positively correlated for all ICs (see Table S1 for details), suggesting that SD- and MSSD-measured brain variability are highly consistent in rsfMRI data.

Table S1. *Pearson correlations between brain variability measured by SD and MSSD.*

ICs	Correlation between SD and MSSD	
	r	p
IC1	**0.735**	**< .0001**
IC2	**0.821**	**< .0001**
IC3	**0.723**	**< .0001**
IC4	**0.664**	**< .0001**
IC5	**0.648**	**< .0001**
IC6	**0.835**	**< .0001**
IC7	**0.789**	**< .0001**
IC8	**0.506**	**< .0001**
IC9	**0.680**	**< .0001**
IC10	**0.857**	**< .0001**
IC11	**0.714**	**< .0001**

Note. IC = Independent component, SD = standard deviation, MSSD = mean squared successive difference.

Resting-state BOLD variability and individual differences in metacontrol

SD and MSSD of all ICs revealed negative correlations with RAT performance. SD of all selected components was not significantly related with RAT scores. We found a significant negative correlation between the MSSD of IC3 (i.e., frontal motor regions) and the RAT score (r = -0.350, $p_{uncorrected}$ = 0.003, $p_{corrected}$ < 0.05) (see Figure S8 and Table S2).

AUT flexibility and fluency scores were not significantly associated with brain variability.

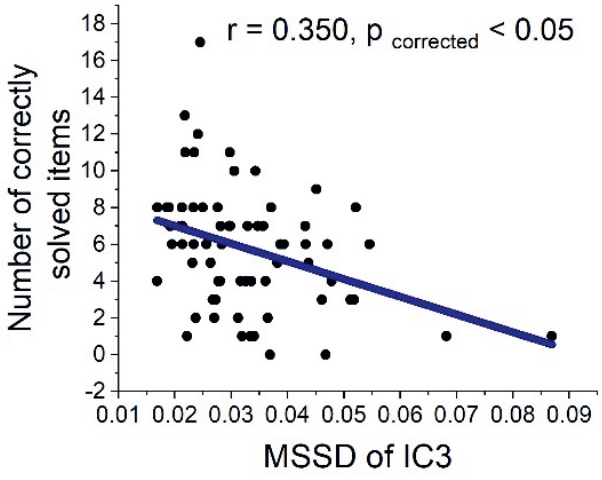

Figure S8. RAT performance was significantly negatively correlated with brain variability of the frontal motor regions (i.e., IC3). Brain variability was measured by MSSD.

Table S2. *Correlations between brain variability measured by SD, MSSD, and metacontrol policies measured by RAT scores, AUT flexibility scores, and AUT fluency scores.*

Brain variability measures	ICs	RAT scores			AUT flexibility scores			AUT fluency scores		
		r	$p_{uncorrected}$	$p_{corrected}$	r	$p_{uncorrected}$	$p_{corrected}$	r	$p_{uncorrected}$	$p_{corrected}$
SD	IC1	-0.166	0.173	1.000	0.002	0.987	1.000	-0.100	0.413	1.000
	IC2	-0.163	0.181	1.000	-0.205	0.091	1.000	-0.215	0.076	1.000
	IC3	-0.205	0.090	1.000	-0.138	0.257	1.000	-0.227	0.061	1.000
	IC4	-0.162	0.184	1.000	-0.088	0.471	1.000	-0.121	0.323	1.000
	IC5	-0.004	0.977	1.000	-0.133	0.275	1.000	-0.081	0.507	1.000
	IC6	-0.202	0.096	1.000	-0.146	0.231	1.000	-0.061	0.620	1.000
	IC7	-0.053	0.665	1.000	-0.174	0.152	1.000	-0.136	0.264	1.000
	IC8	-0.002	0.988	1.000	-0.040	0.744	1.000	-0.119	0.331	1.000
	IC9	-0.129	0.292	1.000	-0.101	0.409	1.000	-0.080	0.514	1.000
	IC10	-0.274	0.023	1.000	-0.244	0.044	1.000	-0.262	0.030	1.000
	IC11	-0.165	0.177	1.000	-0.204	0.093	1.000	-0.143	0.242	1.000
MSSD	IC1	-0.268	0.026	1.000	-0.128	0.294	1.000	-0.050	0.681	1.000
	IC2	-0.301	0.012	1.000	-0.260	0.031	1.000	-0.174	0.153	1.000
	IC3	**-0.350**	**0.003**	**0.033**	-0.251	0.037	1.000	-0.150	0.218	1.000
	IC4	-0.151	0.216	1.000	-0.129	0.289	1.000	-0.103	0.399	1.000
	IC5	-0.181	0.136	1.000	-0.196	0.106	1.000	-0.017	0.892	1.000
	IC6	-0.231	0.056	1.000	-0.186	0.126	1.000	-0.077	0.527	1.000
	IC7	-0.149	0.223	1.000	-0.267	0.027	1.000	-0.253	0.036	1.000
	IC8	-0.205	0.091	1.000	-0.201	0.097	1.000	-0.104	0.395	1.000
	IC9	-0.188	0.122	1.000	-0.242	0.045	1.000	-0.099	0.417	1.000
	IC10	-0.267	0.027	1.000	-0.181	0.136	1.000	-0.115	0.348	1.000
	IC11	-0.193	0.113	1.000	-0.222	0.067	1.000	-0.050	0.683	1.000

Note. IC = Independent component, SD = standard deviation, MSSD = mean squared successive difference, RAT = Remote Associates Task, AUT = Alternate Uses Task, P corrected = Bonferroni corrected p value. Spearman correlation was used for correlation analyses.