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

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Chapter 1

General Introduction

Cognitive control and metacontrol

Cognitive control, also known as executive control or executive functions, refers to a set of mental processes that enable individuals to regulate their thoughts and actions to achieve specific goals and adapt to changing circumstances (Botvinick et al., 2001; Braver, 2012; E. K. Miller, 2000; Scherbaum et al., 2011). It involves a wide range of mental processes, including goal representation and maintenance, working memory, attention, stimulus-response mapping, and flexible adaptation to changing conditions (Egner, 2007; Kieras et al., 2000; Mackie et al., 2013). Cognitive control is a key aspect of higher-order cognitive functions and plays a crucial role in various aspects of daily life, planning, problem-solving, and decision-making (Botvinick et al., 2001; Diamond, 2013; E. K. Miller & Cohen, 2001). Impairments in cognitive control processes can manifest in various neurodevelopmental disorders and psychiatric conditions, like attention-deficit/hyperactivity disorder (ADHD) (Willcutt et al., 2005), obsessive-compulsive disorder (OCD) (Chamberlain et al., 2008), and schizophrenia (Lesh et al., 2011).

Traditional approaches on the functioning of cognitive control assume the existence of a relatively unitary control system, which serves to overcome action tendencies induced by automatic processes (Botvinick et al., 2001; E. K. Miller & Cohen, 2001; Norman & Shallice, 1986). However, increasing functional, neural, and computational evidence indicates that cognitive control likely emerges from the interplay of probably two antagonistic systems or components. Goschke (2003) discussed how humans often face control dilemmas that involve balancing persistence and flexibility in control and behavior. Furthermore, Cools and colleagues have identified two separable dopaminergic pathways: the mesofrontal pathway, originating in the ventral tegmental area and targeting the prefrontal cortex, and the nigrostriatal pathway, originating in the substantia nigra and targeting the striatum (Cools, 2006, 2008; Cools & D'Esposito, 2011). Using a modeling-based approach, Durstewitz & Seamans (2008) have revealed that the dominance of dopaminergic D1- class receptors in prefrontal cortex supports information maintenance, while the dominance of D2- class receptors is beneficial for mental flexibility.

In recent developments, Hommel (2015) introduced the metacontrol model, positing that people can vary in their cognitive processing style along a dimension characterized by two poles: “persistence” on one end and “flexibility” on the other (Figure

1). A high degree of persistence emphasizes a strong focus on the current task goal and the information related to it (Hommel, 2015; Hommel & Colzato, 2017c). In contrast, a high degree of flexibility is characterized by an open-minded approach and inclusive processing that considers alternative goals and information related to them, thereby facilitating switching between tasks, ideas, and actions (Hommel, 2015; Hommel & Colzato, 2017c). Truly adaptive control requires humans to find a balance between persistence and flexibility, an ability called metacontrol (Hommel, 2015). Regarding processing characteristics, a metacontrol bias toward persistence is characterized by a strong impact of the current goal(s) and by a high degree of competitiveness between alternatives, whereas flexibility is characterized by a weak impact of goal(s) and mild competitiveness between alternatives (Hommel, 2015; Hommel & Colzato, 2017c) (Figure 1).

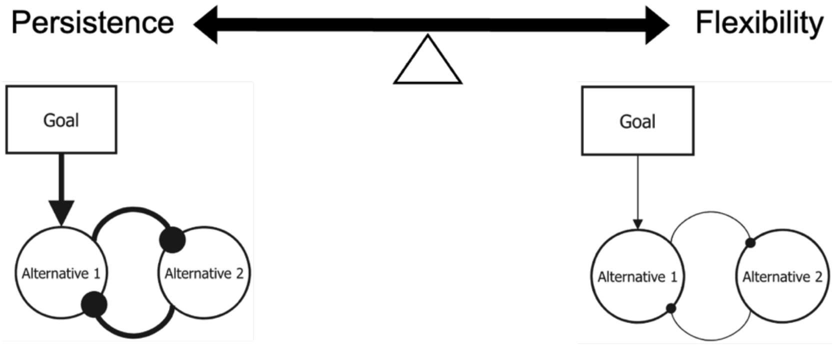

Figure 1. Key assumptions of the Metacontrol State Model (figure modified from Hommel, 2015)

Interestingly, there are systematic individual differences with respect to the default state of metacontrol. Differences in genetic disposition and cultural background have been associated with systematic interindividual variability in metacontrol biases toward persistence or flexibility. Moreover, metacontrol also shows intraindividual differences, with individuals continuously adjusting their bias toward persistence or flexibility in response to the specific demands of a given task. Several factors have been shown to impact metacontrol biases, including mood (Dreisbach & Goschke, 2004), meditation-induced states (Colzato et al., 2017), and reward (Hefer & Dreisbach, 2016, 2017).

Neural “noise”

Noise can be defined as “random or irregular fluctuations or disturbances that are not part of a signal, interfere with or obscure a signal, or more generally, any distortions or additions that interfere with the transfer of information”(Faisal et al., 2008). Within the context of the central nervous system (CNS), neural noise can be described as the signal-to-noise ratio. The CNS’s noise level can be assessed based on the ratio of signal strength to random background or noise activity (Faisal et al., 2008). Recent work has also characterized noise as the variability resulting from “random or unpredictable fluctuations and disturbances” (McDonnell & Ward, 2011).

While noise is typically assumed to degrade performance, it can sometimes enhance information processing in non-linear systems. For instance, stochastic resonance, a phenomenon in which threshold-like systems can enhance their capacity to detect and transmit weak, often periodic signals by introducing a certain level of noise (McDonnell & Ward, 2011; Moss et al., 1994). At low noise levels, the sensory signal fails to surpass the system’s threshold, resulting in the detection of only a few signals. Conversely, at high noise levels, the noise tends to dominate the system’s response. However, at intermediate noise intensities, noise facilitates the signal in reaching the threshold without overpowering it. Over the past few decades, the field of neuroscience has witnessed an increase in experimental research and biologically detailed modeling focusing on stochastic resonance (Gluckman et al., 1996; McDonnell & Ward, 2011; Moss et al., 2004).

Neural noise is an inherent aspect of the nervous system, and exists in sensory perception, information transmission, higher-level cognitive processing, motor responses, and overall information processing (Ermentrout et al., 2008; Faisal et al., 2008; McDonnell & Ward, 2011). In this thesis, we use the broad term “noise” to indicate two specific aspects of brain activity in the nervous system: moment-to-moment variability observed in the blood oxygen level-dependent (BOLD) signal, and aperiodic neural activity that reflects arrhythmic patterns of EEG signals. Over the last decades, both BOLD signal variability and aperiodic neural activity have long been neglected or regarded as “noise” with little physiological significance. Recent research, however, has begun to shed light on their cognitive relevance and functional role in reflecting human behavior and cognitive functions (Donoghue et al., 2020; Garrett et al., 2010, 2011, 2013, 2018; Pertermann, Mückschel, et al., 2019; Voytek et al., 2015; Waschke, Kloosterman, et al., 2021). This thesis aims to explore whether and how BOLD signal variability and aperiodic neural activity are associated with higher-level cognitive functions, specifically focusing on the metacontrol bias toward persistence or flexibility.

Temporal variability of fMRI signals

The conventional approach to analyzing functional magnetic resonance imaging (fMRI) data involves examining "activation" patterns resulting from analyses of averaged signals within voxels and within individuals (Friston et al., 1994). While this approach has undoubtedly advanced our understanding of the brain function, it is important to acknowledge that the brain's inherent state is variable (Faisal et al., 2008; Raichle, 2010). A substantial amount of research has been conducted on the presence of moment-to-moment variability in brain activity (Biswal et al., 1995; Faisal et al., 2008; Stein et al., 2005). However, few studies have recognized this variability as a meaningful aspect of brain function or explored it as a valuable measure of individual differences.

Recent work has revealed the potential of BOLD variability-based brain patterns as powerful indicators of age (Garrett et al., 2010; Samanez-Larkin et al., 2010). Garrett et al. (2010) discovered that the age-predictive power of the variability-based pattern was over five times greater than that of the mean-based pattern, and that there were virtually no overlapping spatial patterns between the variability-based brain patterns and the mean-based brain patterns. This challenges the traditional view of BOLD variability as undesirable "noise" in fMRI data, indicating the presence of meaningful variance-based "signal". Moreover, an increasing number of fMRI studies have uncovered an association between temporal variability of fMRI signals and behavior. For instance, higher levels of BOLD variability have been associated with higher accuracy, faster and more stable responses across a range of tasks, including those involving perception, attention, working memory, and task switching (Armbruster-Genç et al., 2016; Garrett et al., 2011, 2013; Grady & Garrett, 2018; Guitart-Masip et al., 2016; Millar et al., 2021). In addition to marking individual differences on a single task, there is evidence to suggest that moment-to-moment BOLD variability relates to behavior in a "trait-like" way. For example, a previous study found consistent negative associations between BOLD variability and both mean response time and response time standard deviation across four different tasks, spanning both young and older age groups (Grady & Garrett, 2018).

Regarding the measurements of temporal variability of fMRI signal, there exist various approaches, including variance (He et al., 2010), standard deviation (SD)(Garrett et al., 2010, 2013), and mean square successive differences (MSSD)(Leo et al., 2012; Samanez-Larkin et al., 2010). Each of these metrics provides insights into different facets of the temporal dynamics of brain activity. SD, the square root transformation of variance, represents the width of a neural time series' distribution. SD of the BOLD signal has been a widely used metric in previous studies. A higher SD of the BOLD signal has been related to more accurate and faster responses across a range of cognitive tasks (Armbruster-Genç et al., 2016; Garrett et al., 2011, 2013, 2014; Waschke, Kloosterman, et al., 2021). MSSD (Neumann et al., 1941) calculates the average squared difference between consecutive time points in the BOLD signal time course. Recent work has employed MSSD as a measure of BOLD signal variability, revealing connections between MSSD of the BOLD signal and functional connectivity (Baracchini et al., 2021), cognitive functions (Boylan et al., 2021), and psychiatric disorders (Easson & McIntosh, 2019; Zhang et al., 2021).

Aperiodic neural activity

Electroencephalography (EEG) is one of the widely used techniques to noninvasively investigate the dynamics of human brain function. Over the last decades, the focus has been on neural oscillations (i.e., periodic activity), which are the rhythmic activity patterns of EEG signals that reflect synchronized fluctuations of cortical microcircuits. Neural oscillations have been shown to be involved in various cognitive and behavioral processes, such as attention (Busch & VanRullen, 2010; Klimesch, 2012), memory (Klimesch, 1999), and cognitive control (Cavanagh & Frank, 2014). However, besides the rhythmic patterns, there exist arrhythmic patterns, referred to as the non-oscillatory or aperiodic component, in EEG power spectra.

The aperiodic component is often referred to as background activity or "scale-free" broadband activity, which exhibits a $1/f$-like distribution with decreasing spectral power across increasing frequencies (Donoghue et al., 2020; He, 2014; Pritchard, 1992). This component can be mathematically described by a $1/f^x$ function, where ‘f’ represents the frequency and ‘x’ denotes an exponent that determines the steepness of the decrease in power across frequencies (Donoghue et al., 2020; K. J. Miller et al., 2009; Voytek et al., 2015). In the EEG power spectrum, the aperiodic component can be characterized by the aperiodic exponent (x, 1/*f* slope) and aperiodic offset. The aperiodic exponent, also called 1/*f* slope, is a key feature of aperiodic activity. It is analogous to the negative slope of the log-log transformed power spectrum, reflecting the steepness (or slope) of the decay of power across frequencies (Donoghue et al., 2020). A smaller aperiodic exponent (flatter 1/f slope) indicates that the distribution of power across frequency bands is more equal, with relatively more power in the higher frequencies. In contrast, a larger aperiodic exponent (steeper 1/f slope) means that power decreases more quickly with frequency, thus showing a dominance of lower frequencies in the power distribution. Meanwhile, the aperiodic offset denotes the broadband shift in power across frequencies (Donoghue et al., 2020).

The aperiodic component is often referred to as “noise” because it captures the non-oscillatory component of the EEG signal, which was traditionally considered as background noise in contrast to the more meaningful oscillatory components (i.e., periodic activity such as alpha or beta waves). However, growing evidence has shown that the aperiodic component of the EEG signal can carry meaningful information related to neural and cognitive processes. Recent research reveals the cognitive importance of the aperiodic component, as well as its developmental and clinical relevance (Adelhöfer, Paulus, et al., 2021; Donoghue et al., 2020; Gyurkovics et al., 2022; He et al., 2010; Hill et al., 2022; Huang et al., 2017; Merkin et al., 2023; Münchau et al., 2021; Ostlund et al., 2021; Pertermann, Bluschke, et al., 2019; Shuffrey et al., 2022; Virtue-Griffiths et al., 2022; Voytek et al., 2015; Wainio-Theberge et al., 2021). For instance, Voytek et al. (2015) identified a flattened 1/*f* slope (reduced aperiodic exponent values) in older adults compared to younger adults. Ostlund et al. (2021) observed a more flattened EEG power spectrum (smaller aperiodic exponents) in adolescents with ADHD relative to their typically developing peers. Further emphasizing its cognitive importance, Virtue-Griffiths et al. (2022) detected an increase in the aperiodic exponent at frontocentral electrodes from the baseline to the delay period in the working memory task. Furthermore, investigations focusing on stimulus-induced changes in 1/*f* activity reported a more substantial increase in the exponent when participants encountered a rare oddball stimulus immediately after a frequent standard stimulus (Gyurkovics et al., 2022). Notably, Pertermann et al. reported an increased exponent (steeper 1/*f* slope) during the controlled inhibition of a prepotent response (Pertermann, Bluschke, et al., 2019; Pertermann, Mückschel, et al., 2019). Together, these studies provide strong evidence for the functional relevance of aperiodic activity in the EEG power spectrum to human behavior and cognitive functions.

Knowledge gap and research questions

Emerging evidence has indicated that what was historically regarded as "noise" – namely, the temporal variability of fMRI signals and the aperiodic component in the EEG power spectrum – plays a crucial functional role in understanding human behaviors. However, it is largely unknown whether these neural parameters are associated with higher-level cognitive functions, particularly different metacontrol biases. Exploring the relationships between BOLD signal variability, aperiodic activity, and metacontrol can not only enhance our understanding of the functional importance of these traditionally termed "noise" parameters but also provide insights into the neural foundations of metacontrol.

In this thesis, we aim to address three central questions:

1. How are individual differences in BOLD signal variance related to different metacontrol styles? While many studies have indicated the positive impact of BOLD signal variability on tasks and behaviors relying on cognitive flexibility (Armbruster-Genç et al., 2016; Garrett et al., 2011, 2013; Grady & Garrett, 2018; Guitart-Masip et al., 2016; Millar et al., 2021), it is yet to be determined whether the positive effect of BOLD signal variability also holds for cognitive persistence. Moreover, previous research has identified associations between on-task neural variability and cognitive functioning (Armbruster-Genç et al., 2016); however, it remains unclear whether *off*-task variability is systematically linked to individual cognitive control styles. This thesis, therefore, aims to explore the association between the individual's resting-state BOLD signal variability and individual differences in metacontrol biases toward persistence or flexibility.

2. Is the broadband aperiodic activity in the EEG power spectrum associated with metacontrol biases? Although aperiodic neural activity has been demonstrated to relate to human behavior and cognition (Donoghue et al., 2020; Pertermann, Bluschke, et al., 2019; Voytek et al., 2015), its relevance for higher-level cognitive functions is only beginning to be understood. This thesis aims to investigate whether the broadband aperiodic activity in the EEG power spectrum is associated with demand-specific biases of metacontrol toward persistence or flexibility.

3. Is aperiodic neural activity associated with different types of creative thinking, namely divergent and convergent thinking, that rely on metacontrol? Divergent thinking, with its emphasis on generating and switching between novel ideas, benefits from a metacontrol bias toward flexibility (Zhang et al., 2020). Conversely, convergent thinking, aiming to discover the unique correct solution, benefits from a metacontrol bias toward persistence (Zhang et al., 2020). Is there a relationship between aperiodic activity and creative processes? Could the aperiodic activity act as a neural correlate of creativity? This thesis delves into the potential role of aperiodic activity in creative thinking, investigating how it may relate to divergent and convergent thinking processes.

Overview of this thesis

The research presented in this thesis explores the relationship between traditionally defined neural “noise” – specifically, the BOLD signal variability and the aperiodic component of the EEG power spectrum – and its connection to metacontrol. The following three chapters describe empirical studies that delve into this association at both the inter-individual and intra-individual levels. **Chapter 2** presents a study that explores the association between resting-state BOLD signal variability and individual differences in metacontrol styles (i.e., persistence vs. flexibility). **Chapter 3** investigates the relationship between the aperiodic component of the EEG power spectrum and different metacontrol states or the dynamic of metacontrol adjustments. **Chapter 4** delves into creativity and investigates the association between aperiodic neural activity and two types of creative thinking: divergent thinking (DT) and convergent thinking (CT). Finally, **Chapter 5** summarizes this thesis and discusses theoretical and practical implications. Furthermore, this chapter identifies the limitations of the studies presented and suggests directions for future research.